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A STUDY OF HYBRIDIZATION BETWEEN TWO SPECIES OF
COREGONINE FISHES, *Coregonus clupeaformis* (MITCHILL)
AND *C. artedii* LESUEUR IN ALBERTA

by



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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled A STUDY OF HYBRIDIZATION BETWEEN TWO SPECIES OF COREGONINE FISHES, *Coregonus clupeaformis* (MITCHILL) and *C. artedii* LESUEUR IN ALBERTA submitted by Martin Joseph Paetz in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Frontispiece. Photograph of cisco (upper), lake whitefish (lower) and lake whitefish-cisco hybrid (middle), from Utikuma Lake.



ABSTRACT

Coregonus clupeaformis (MITCHILL) and *C. artedii* LESUEUR are sympatric in many of the lakes in the Peace and Athabasca drainage basins in Alberta. It has been observed by commercial fishermen that a form of whitefish intermediate in external appearance between *C. clupeaformis* and *C. artedii* exists in certain lakes where both species are present, but this form has never been reported in lakes where only one whitefish species occurs.

Morphological and electrophoretic analyses of sympatric and allopatric populations revealed that an intermediate form does exist in five of the seven lakes which contain sympatric populations. Evidence from these analyses and from artificial breeding experiments is presented to show that the intermediate form is a result of hybridization between the two species. Presumed F_1 hybrids made up 6% of the combined populations in Utikuma Lake while the percentage of hybrids in other lakes was considerably less than 6%.

In two of the lakes studied, *C. artedii* occurs as a dwarf form while *C. clupeaformis* is normal. No hybrids were found in these situations. No whitefish similar in morphometric characteristics or electrophoretic patterns to those of hybrids were found in lakes where either species occurs in allopatry.

Segregation at spawning time, or due to habitat preference, is not well developed in lakes where hybridization takes place. Temporal isolation is more apparent in those lakes in which *C. artedii* occurs in dwarf form but some overlap with *C. clupeaformis* spawning does exist. Where segregation in spawning time was noted, i.e. in Touchwood Lake and Cold Lake, *C. clupeaformis* had virtually completed spawning prior to the onset of spawning of *C. artedii*.

Artificial crosses of the parent species failed to show any effective post mating isolating mechanism. This was equally true whether the parents were from lakes in which hybrids were found or from lakes where no hybrids occur. Artificial backcrosses involving presumed hybrid males and females of both parent species from Utikuma Lake and Nipisi Lake were successfully produced. Backcrossing involving female hybrids was unsuccessful. The opportunity from introgression is reduced by the scarcity of F_1 hybrids, lack of gonad development in a significant percentage of hybrids and sterility of female hybrids.

Environmental factors or human interferences such as watershed alteration and commercial fishing do not play important roles in natural hybridization of the two species under study.

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INTRODUCTION

Hybridization, as applied to this study, refers to the interbreeding of individuals of two different species, as a result of imperfect development of isolating mechanisms. It is considered a relatively common phenomenon in groups of animals, particularly in freshwater fishes in the northern regions (Mayr 1963). Hubbs (1955) reports on numerous examples of natural hybridization in freshwater fishes but states that examples of hybridization in marine fishes is relatively rare. In the past two or three decades a number of authors have examined in detail, cases of interspecific, as well as intergeneric hybridization. Nelson (1968) examined hybridization in two species of suckers (Catostomidae). Stewart (1966), Hubbs (1956), Hubbs and Strawn (1956), Aspinwall (1968) and others, have examined hybridization in various species of minnows (Cyprinidae). Many studies deal with artificial hybridization between species which may not hybridize in their natural environment. Nelson (1968) states that most works on natural hybridization deal with cases where one or both of the parental species were introduced or when the environment had been altered by man; and further that most studies on isolating mechanisms in fish deal with species which never or rarely hybridize naturally.

The hybridization of whitefish species in Swedish waters has been studied for more than twenty years (Svardson 1965). In these studies, experimental work produced: F_1 and F_2 generations

of hybrids using *Coregonus oxyrhynchus* (Linnaeus) and *Coregonus nasus* (Pallas) as parents, F₁ and F₂ generations using *C. pidschian* (Gmelin) and *C. peled* (Gmelin), and F₁ and F₂ and F₃ generations using *C. oxyrhynchus* and *C. albula* (Linnaeus) parents. In addition to these artificial hybridization experiments Svardson (1957) presents evidence of spontaneous introgression of whitefish and cisco populations in natural situations. He states: "In environments with few ecological niches the process has gone very far, reaching replacement or complete fusion of populations."

Gasowska (1958) refers to the summarization by L. S. Berg on the occurrence of natural interspecific hybrids of the genus *Coregonus* and deals specifically with the morphology, growth and fertility of artificially produced hybrids of *C. lavaretus maraenoides* Polykov x *C. albula* L.

A characteristic often stressed by European workers concerning interspecific hybrids of the genus *Coregonus* is the fertility of these hybrids.

No similar studies on the natural interspecific hybridization of whitefish in North America have been carried out as far as is known. Several successful experiments in artificial hybridization have, however, been performed. Garside and Christie (1962) suggest that the first experimental hybridization of two species of coregonine fishes was probably carried out by Moenkhaus in 1910. He produced reciprocal crosses between whitefish and cisco and obtained viable progeny from both. These authors also successfully produced progeny from reciprocal

crosses of *C. clupearformis* (Mitchill) and *C. artedii* Lesueur and from *C. clupearformis* x *Prosopium cylindraceum* Pallas, but the reciprocal of the latter cross failed as did *C. artedii* x *P. cylindraceum* and its reciprocal.

Koelz (1929) reports the occurrence of "mule whitefish" which were taken occasionally out of many of the Great Lakes ports and which were usually considered to be hybrids between *C. clupearformis* and *C. artedii*. He provides some morphometric and meristic information on one specimen taken at Toledo, Ohio, as well as a sketch of the head showing position of the mouth parts in comparison to that of a normal *C. clupearformis*. Hubbs (1955) mentions hybrids between whitefish and lake herring or cisco of the Great Lakes being found in nature (rarely) and further states that he has interpreted other specimens as interspecific hybrids within the subgenus *Leucichthys*. Hinks (1943) notes that in Lake Winnipeg there are frequently found fish which appear to be intermediate between certain species of ciscoes or even between cisco and whitefish. He further points out that whitefish eggs were successfully fertilized by male cisco and cisco eggs by male whitefish at the Dauphin River hatchery in 1937. Hinks does not mention whether the eggs from these crosses developed and hatched.

Fishes intermediate in characters between the whitefish and the common cisco have occurred in both Lake Erie and Lake Ontario and the specimens examined exhibited a more rapid growth rate than the presumed parent species. These intermediates were

also apparently sterile (W.B. Scott, pers. comm.). Ryder et al (1964) mention finding *C. artedii* x *C. clupeaformis* hybrids in northern Ontario.

The present study is an investigation into hybridization between two recognized species of coregonine fishes, the lake whitefish, *Coregonus clupeaformis* (Mitchill) and the cisco *C. artedii* Lesueur, in Alberta. (Note: Western Canada populations of cisco are sometimes referred to as the *C. artedii* complex, Lindsey pers. comm.). These two species have come together since the Pleistocene glaciation and occur sympatrically in many lakes in the central and northern areas of the Province. Both species have been exploited by commercial fisheries in many though not in all of the lakes in which they are found. Fry and eyed-eggs of lake whitefish were extensively stocked in the Province during the 1940's which resulted in extension of their range into reservoirs of the Bow River drainage. The species was, however, endemic to both the sympatric and allopatric situations studied in this work, prior to any distribution by man. The cisco has not been cultured or transplanted save for one recorded transfer of eyed eggs to Spray Lakes reservoir near Canmore in 1955.

This study has the following objectives. First, to verify that the wild intermediate forms of whitefish are the result of hybridization and to establish methods of identifying them, second, to determine the extent of hybridization in natural populations, and third, to examine the possible isolating mechanisms and consider their effectiveness in this particular case.

DESCRIPTION OF THE STUDY AREA

Field collections of fish specimens and physical lake data were obtained from seven lakes in which lake whitefish and ciscoes occur sympatrically, two lakes in which only ciscoes occur and one lake in which only the lake whitefish is present. All lakes lie within the zone of sympatry of *C. clupeaformis* and *C. artedii* but are located in three separate drainage basins - the Peace, Athabasca and Churchill River systems (Figure 1). The lakes from which populations were sampled are the following:

Peace Drainage

1. Utikuma Lake (Figure 2) is located at $55^{\circ} 50' \text{ N.}$ and $115^{\circ} 25' \text{ W.}$ It has an area of 27,558.1 hectares, a maximum depth of 5.5 meters and mean depth of approximately 2.7 meters. The Utikuma River drains into the west side of the lake via Gift Lake and Utikumasis Lake and drains out on the north shore to eventually join the Wabasca River. Utikumasis Lake is located 6.4 km. upstream from Utikuma Lake and the river between permits free passage of fish. During the study, whitefish and ciscoes were extremely abundant in this connecting stream from late October to early December and were using it as a spawning area. Some of the fish obtained for experimental crossing of the two species were captured in this stream and observations on spawning were also made here. It is somewhat surprising to find that a lake as shallow as Utikuma Lake supports very large populations of

FIGURE 1. Map of Alberta showing zone of sympatry of *C. clupeaformis* and *C. artedii* and zone of *C. clupeaformis* in allopatry. Locations of study lakes indicated by numbers. Circled numbers denote allopatric *C. clupeaformis*, numbers in squares show allopatric *C. artedii* and plain numbers indicate sympatric populations.

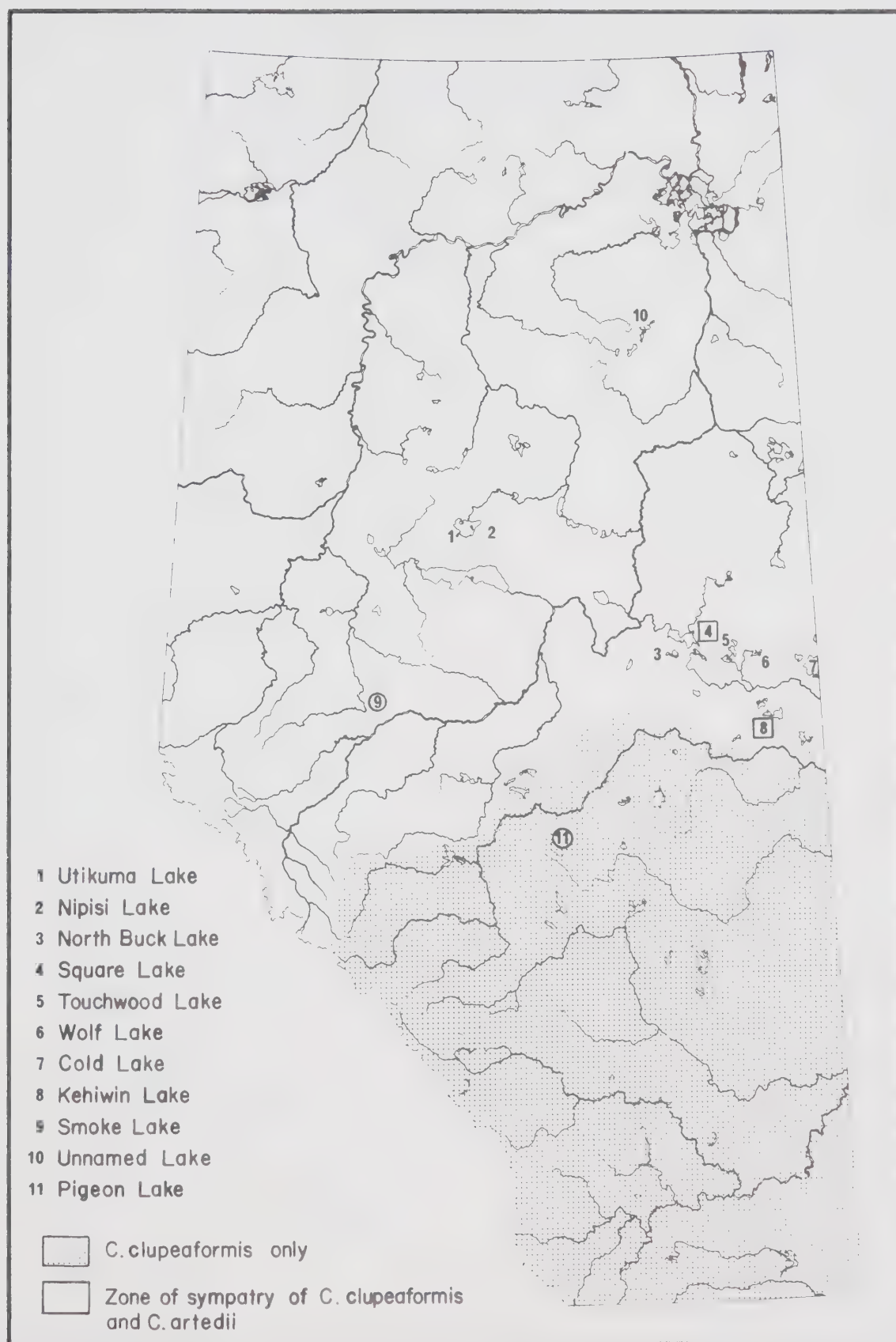
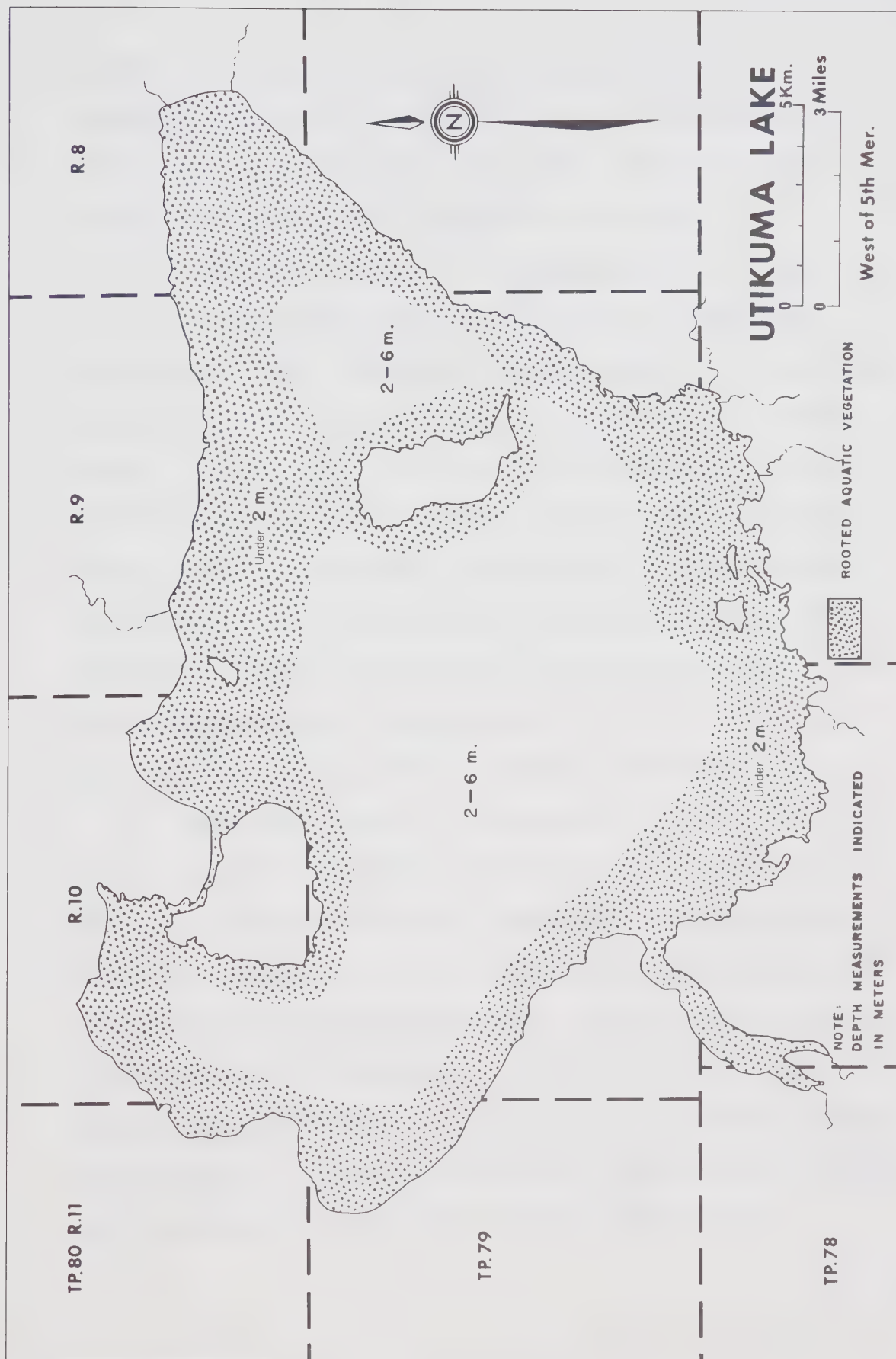


FIGURE 2. General Features of Utikuma Lake.



whitefishes. Emergent rooted aquatic growth extends over an estimated 20 per cent of the area of the lake. The ciscoes in Utikuma Lake are of relatively large size. Adults are only slightly smaller than lake whitefish of the same age.

2. Nipisi Lake (Figure 3) is located at $55^{\circ} 47' \text{ N.}$ and $114^{\circ} 57' \text{ W.}$ approximately 16.1 km. southeast of Utikuma Lake. It has an area of 2,284.1 hectares, a maximum depth of 7.3 meters and a mean depth of 2.7 meters. Two small streams drain surrounding muskegs into the lake. The Nipisi River flows out of the lake in a northerly direction into the Wabasca River system. The main spawning area for whitefishes is a shoal with firm sandy bottom near the east shore. Both species are present in the lake and are exploited by commercial fishermen. The adult size of both species is roughly comparable. The records of the fishery indicate that lake whitefish undergo marked fluctuations in abundance.

3. Smoke Lake (Figure 4) is located at $54^{\circ} 22' \text{ N.}$ and $116^{\circ} 56' \text{ W.}$ A small, low-gradient inlet stream enters the lake at the southeast end and several short, intermittent in-flows are found around the perimeter. The outlet creek drains from the west side of the lake to the Little Smoky River. The lake has a surface area of approximately 971.3 hectares, a maximum depth of 7.6 meters and a mean depth of 3.6 meters. Smoke Lake is in an advanced state of eutrophication. It supports an allopatric population of *C. clupeaformis* which has been only periodically exploited commercially.

FIGURE 3. Nipisi Lake showing general features and morphometry.
(Contours in meters)

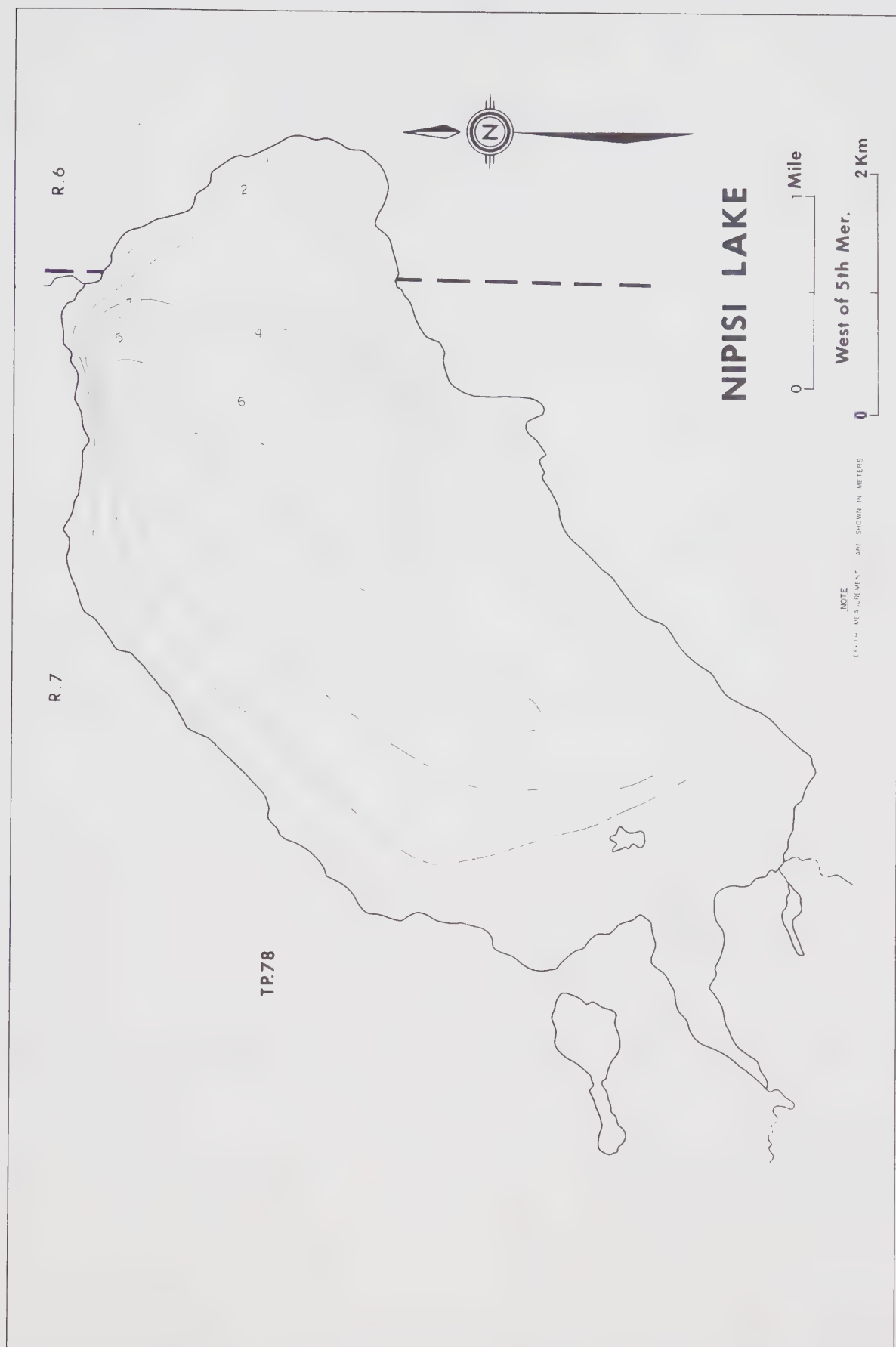
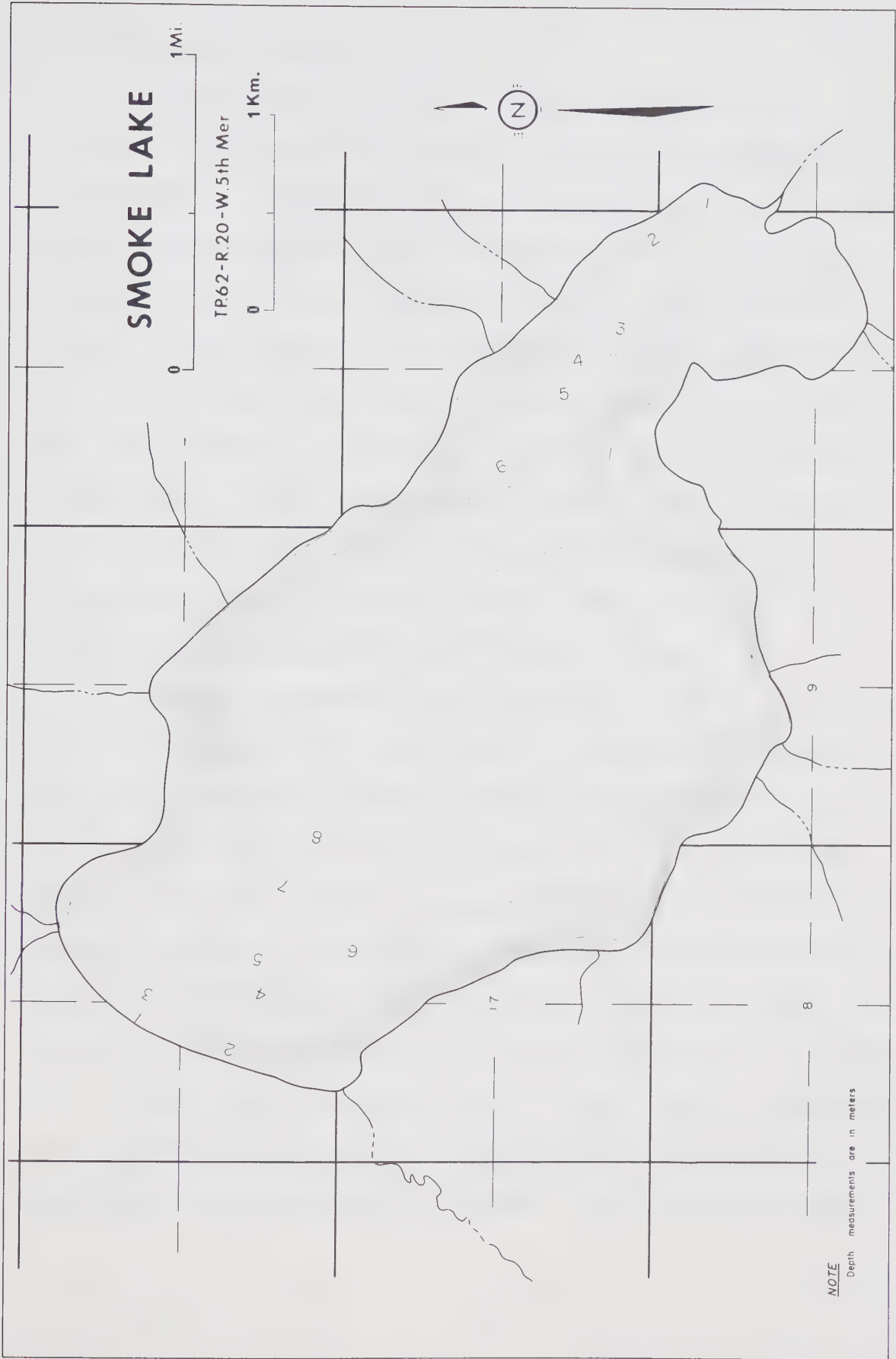


FIGURE 4. Smoke Lake showing general features and morphometry.
(Contours in meters)



Athabasca Drainage

1. Square Lake (Figure 5) is located at $54^{\circ} 54'$ N. and $111^{\circ} 50'$ W. Drainage into the lake is limited to an intermittent stream which has its origin in two small sloughs just south of the lake. The outlet creek is also intermittent. During periods of high lake levels it drains into the Owl River to Lac La Biche and thence via the La Biche River to the Athabasca River. Square Lake has a surface area of 607 hectares, a maximum depth of 37.2 meters and a mean depth of 12.7 meters. The basin slopes abruptly providing a very limited littoral zone. Marked thermal and chemical stratification is characteristic of this lake during the summer. An allopatric population of small *C. artedii* inhabits this lake and an annual commercial fishery is carried out for this species.

2. Unnamed Lake (Figure 6) is located at $57^{\circ} 38'$ N. and $112^{\circ} 30'$ W. in a geographical feature known as the Birch Hills, approximately 160.9 kilometers northwest of Fort McMurray. The lake has an area of 1578.3 hectares, a maximum depth of 14.9 meters and a mean depth of 5.2 meters. There are no well defined streams entering the lake and the small outlet probably freezes to the bottom during the winter. The drainage out of the lake joins the Ells River which is a tributary to the Athabasca River. The lake is considered to be eutrophic and does not undergo summer stratification. Both *C. clupeaformis* and *C. artedii* are present with the adult ciscoes being somewhat smaller than adult lake whitefish of the same age. The lake was included in

FIGURE 5. Square Lake showing general features and morphometry.
(Contours in meters)

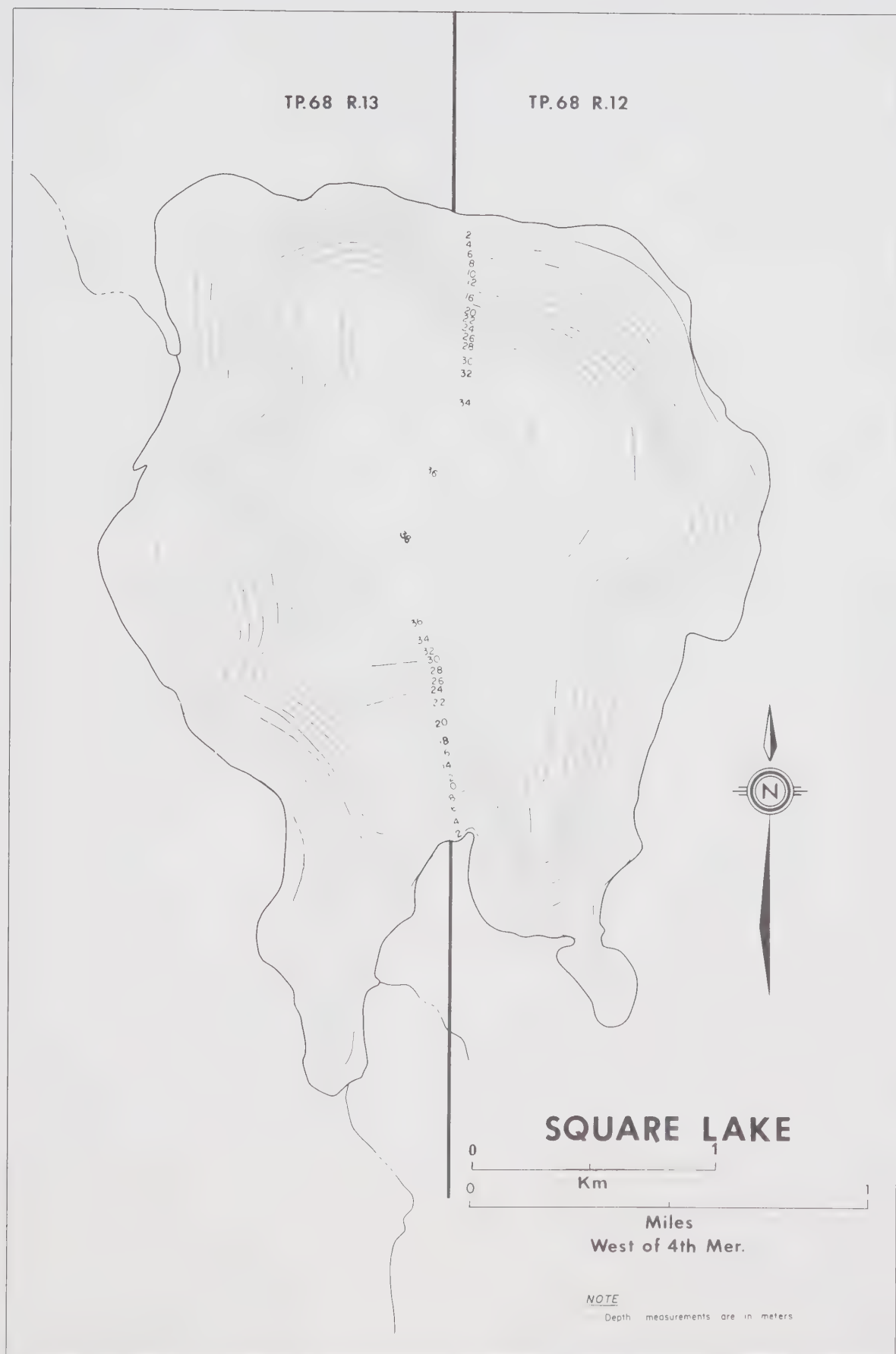
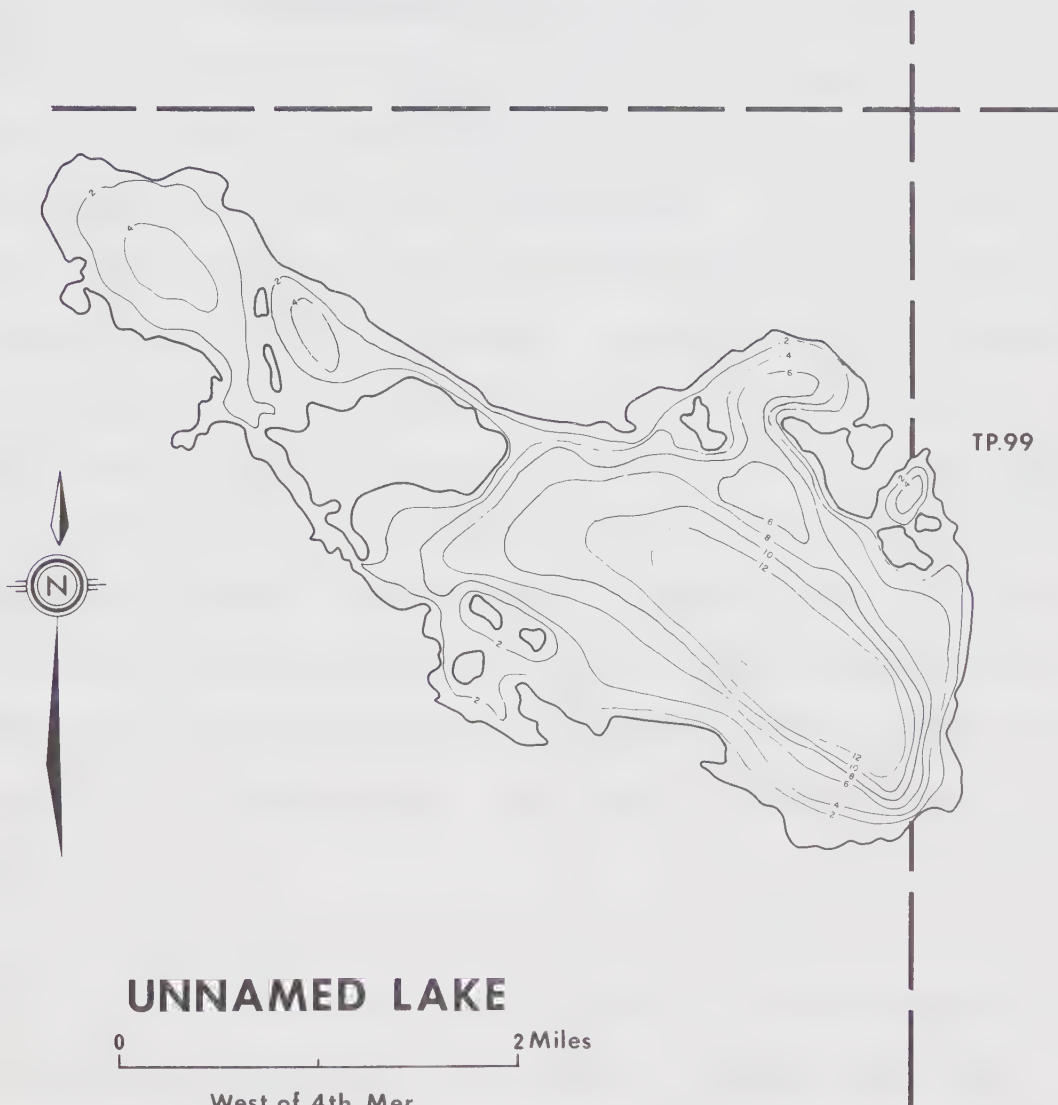


FIGURE 6. Unnamed Lake showing general features and morphometry.
(Contours in meters)

R.16



UNNAMED LAKE

0 2 Miles

West of 4th Mer.

0 3 Km.

NOTE
DEPTH MEASUREMENTS ARE SHOWN IN METERS

the study since there is no record of man's interference either by drainage alteration or by commercial fishing.

Churchill Drainage

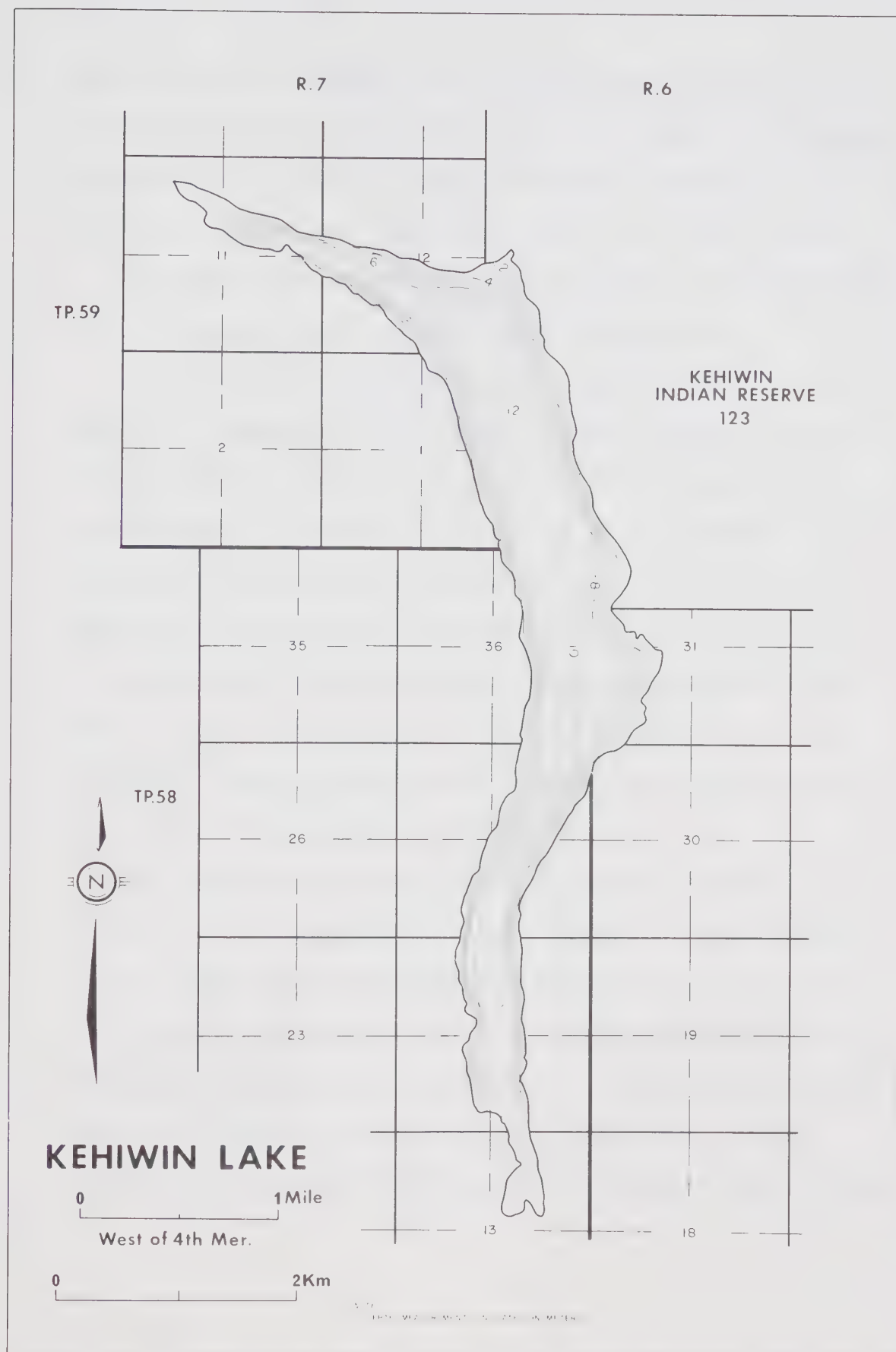
1. Wolf Lake (Figure 7) is located at $54^{\circ} 42'$ N. and $110^{\circ} 57'$ W. and is approximately 30.6 kilometers by road north of Iron River. Drainage into the lake consists of the Wolf River from the north and two small creeks which drain muskeg areas into the northeast arm of the lake. Drainage out of the lake is towards Hudson Bay via the Wolf, Sand, Beaver and Churchill Rivers. Wolf Lake has an area of 3,298.3 hectares, a maximum depth of 39.6 meters and a mean depth of 9.5 meters. The lake may be divided into three areas, a deep trough-like east arm, a central basin of moderate depth and a somewhat shallower northeast arm. It may be considered mesotrophic in nature. Lake whitefish and ciscoes occur in the lake and both are commercially fished. The adult ciscoes are noticeably smaller than lake whitefish though the former are not considered to be dwarfed. Wolf Lake was one of the lakes which received more intensive study.

2. Kehiwin Lake (Figure 8) is located at $54^{\circ} 04'$ N. and $110^{\circ} 54'$ W. It has an area of 627.3 hectares, a maximum depth of 11.6 meters and a mean depth of 6.7 meters. The lake has a long narrow basin and drains by an outlet creek through Bangs Lake and

FIGURE 7. Wolf Lake showing general features and morphometry.
(Contours in meters)



FIGURE 8. Kehiwin Lake showing general features and morphometry.
(Contours in meters)

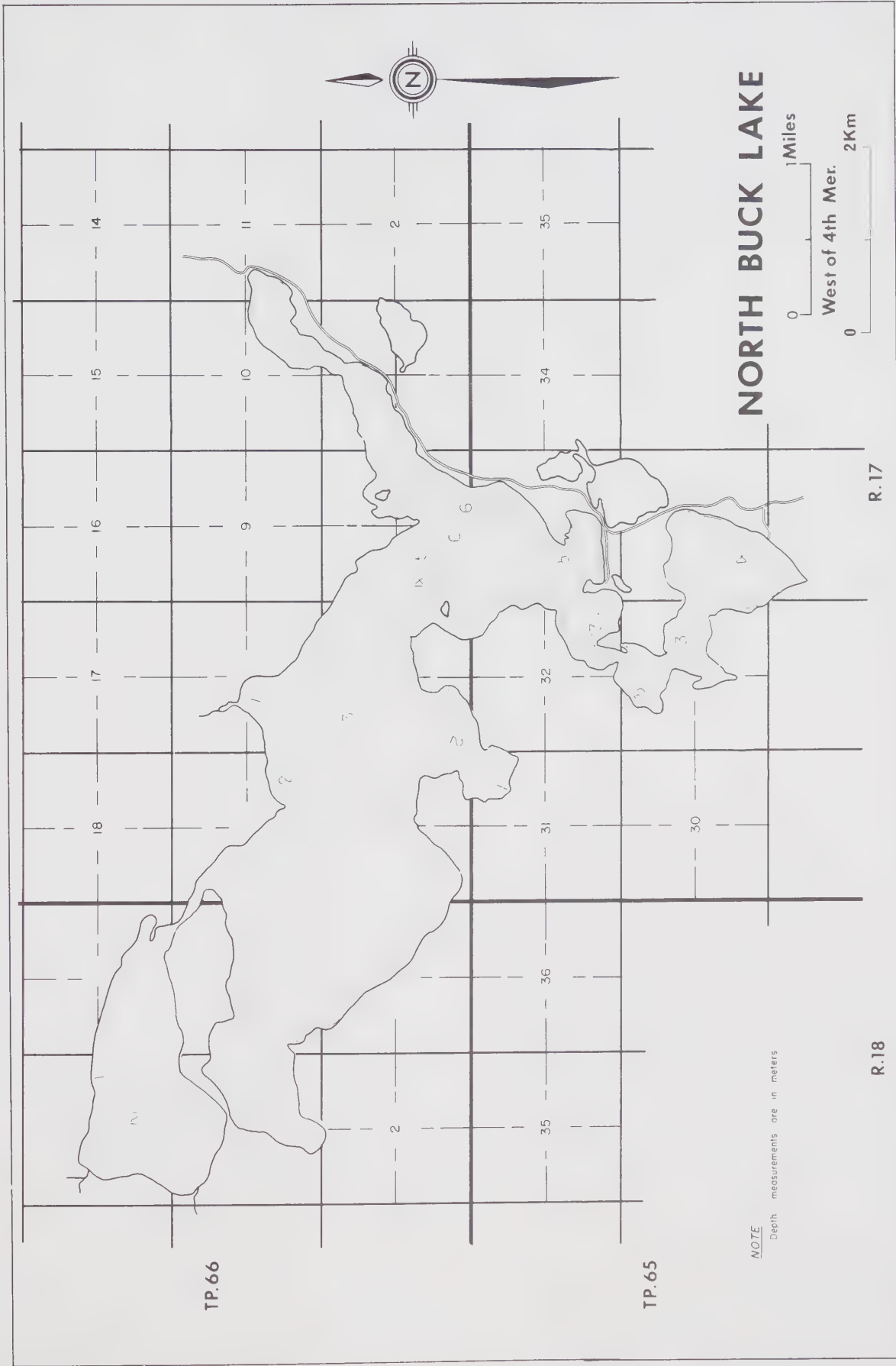


Moose Lake into the Beaver River. Kehiwin Lake is eutrophic but undergoes temporary stratification during the summer. An allopatric population of *C. artedii* is present and some individuals of this population reach a relatively large size. It is surprising that *C. clupeiiformis* which occurs in Moose Lake some 11.3 km. downstream in the drainage system, has not reached Kehiwin Lake.

3. North Buck Lake (Figure 9) is located at $54^{\circ} 41' \text{ N.}$ and $112^{\circ} 32' \text{ W.}$ immediately north of the Village of Caslan. It has an area of 1,753.5 hectares, a maximum depth of 6.1 meters and an average depth of 2.6 meters. During periods of high-water levels the lake has a small drainage outlet to the Amisk River but has no significant inlet streams. North Buck Lake is in advanced stages of eutrophication. Both lake whitefish and ciscoes are present. Adult ciscoes in this lake are similar in size to that of lake whitefish. Gill nets of 14 cm. ($5\frac{1}{2}''$) mesh size are used to capture both species in the annual commercial fishery.

4. Touchwood Lake (Figure 10) is located at $54^{\circ} 49' \text{ N.}$ and $111^{\circ} 23' \text{ W.}$ It has an area of 2,942.1 hectares, a maximum depth of 27.4 meters and a mean depth of 13.7 meters. Drainage into the lake is confined to several small springs and consequently only a very small creek drains out of the lake at the extreme south end. The outlet leads to the Sand River via Seibert Lake. Thermal stratification occurs during the summer and dissolved oxygen values

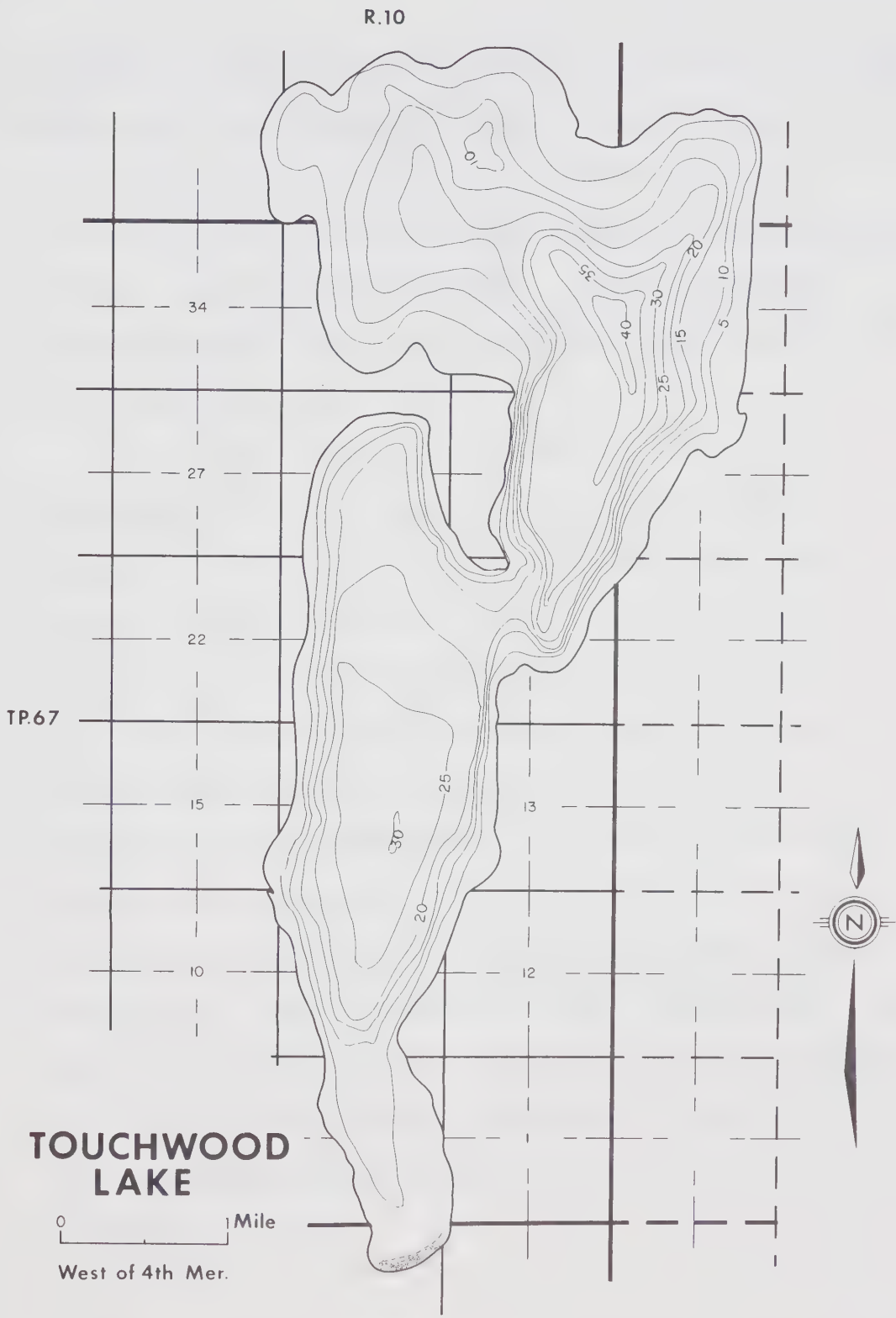
FIGURE 9. North Buck Lake showing general features and morphometry.
(Contours in meters)



NORTH BUCK LAKE

NOTE
Depth measurements are in meters

FIGURE 10. Touchwood Lake showing general features and morphometry.
(Contours in meters)



NOTE

Depth measurements are in meters

are reduced markedly at depths between 9 and 12 meters. Critical oxygen levels may be expected at depths below 18 meters.

C. clupeaformis and *C. artedii* are sympatric in Touchwood Lake but the latter exists in a dwarf form with adults attaining a maximum standard length of 20.5 cm. Commercial fishing is carried out annually for lake whitefish and more or less sporadically for ciscoes.

5. Cold Lake (Figure 11) is located at $54^{\circ} 33'$ N. and straddling $110^{\circ} 05'$ W. It has an area of 23,978.2 hectares, a maximum depth of 99.1 meters and a mean depth of 59.7 meters. Two main tributaries feed into the lake, the Medley River on the northwest and the Martineau River flowing from Primrose Lake to the north. The Cold River leaves the lake on its eastern extremity and continues in an easterly direction to Pierce Lake, and Lac des Isles in Saskatchewan. Cold Lake is oligotrophic. Thermal stratification does occur but the hypolimnion maintains high dissolved oxygen values throughout the period of summer stratification. Both *C. clupeaformis* and *C. artedii* occur in the lake but as in Touchwood Lake, the latter is present as a dwarf form. Lake whitefish have been commercially fished for over 50 years in Cold Lake while ciscoes have only been exploited commercially for approximately 10 years.

FIGURE 11. Cold Lake showing general features and morphometry.
(Contours in meters)

METHODS AND MATERIALS

A. Field Collection and Observations

Specimens of fish were obtained in 1969, 1970 and 1971 by setting braided nylon and monofilament gill nets, but hybrid samples were supplemented by obtaining them from commercial fishermen in some lakes. Virtually all specimens obtained by these methods were adult fish although gill nets with mesh sizes from 5.1 to 14.0 cm. (2" to 5½") stretched mesh, were used in the majority of sets. In the shallow lakes, the presence of relatively large numbers of pike *Esox lucius* Linnaeus, walleye *Stizostedion vitreum* (Mitchill), yellow perch *Perca flavescens* (Mitchill), white suckers *Catostomus commersonii* (Lacepede) and longnose suckers *C. catostomus* Forster, in gill nets of mesh size less than 10.2 cm. (4") stretched mesh, probably prevented them from effectively capturing the younger age classes of lake whitefish and cisco. This problem was alleviated to some extent in deep lakes by the use of floating nets but the success in taking young whitefishes remained minimal. With the exception of the fish which were reared experimentally, therefore, the study is confined to adult specimens.

Since 10 lakes were involved in the study, the volume of material to be preserved would have created major storage difficulties if all coregonines had been kept for analysis.

Therefore, since *C. clupeaformis* and *C. artedii* are easily distinguishable in the field, a minimum of 30 individuals of each of these species with a few exceptions were selected from the sample and transported in ice as soon as possible to the laboratory where they were frozen and retained in this state until detailed examination could be made. All specimens of doubtful classification, i.e. having some degree of intermediacy, were kept and preserved in the same manner as the parent species. Some bias could be introduced by using the 'field selection method' particularly where potential backcrosses are concerned but it was felt that this was reduced by saving for detailed study all specimens which could not readily be identified as either *C. clupeaformis* or *C. artedii*.

For the purpose of establishing a ratio of hybrids to parent stocks in Utikuma Lake, a random sample of 200 coregonines was taken with gill nets in 1971.

Field observations on spawning activities were difficult to make due to two factors. First, the spawning season for whitefishes in the study area is just prior to, or coincident with, or in the case of Nipisi Lake, just after the onset of ice formation. In most cases the ice was not sufficiently thick to support the weight of a person. Second, spawning takes place in late evening or during the night, so that natural light is insufficient to

observe spawning activities. One exception to the above existed in the stream between Utikumasis and Utikuma Lakes. This creek remained free of ice cover during most of the spawning period and was used as a spawning area by lake whitefish and to a lesser extent by ciscoes. Through the use of low intensity artificial light some spawning observations were made in this location.

The majority of the spawning information was collected by gill netting and seining over various time periods prior to, during and after spawning, and by sampling the substrate with an Ekman dredge.

B. Morphological Studies

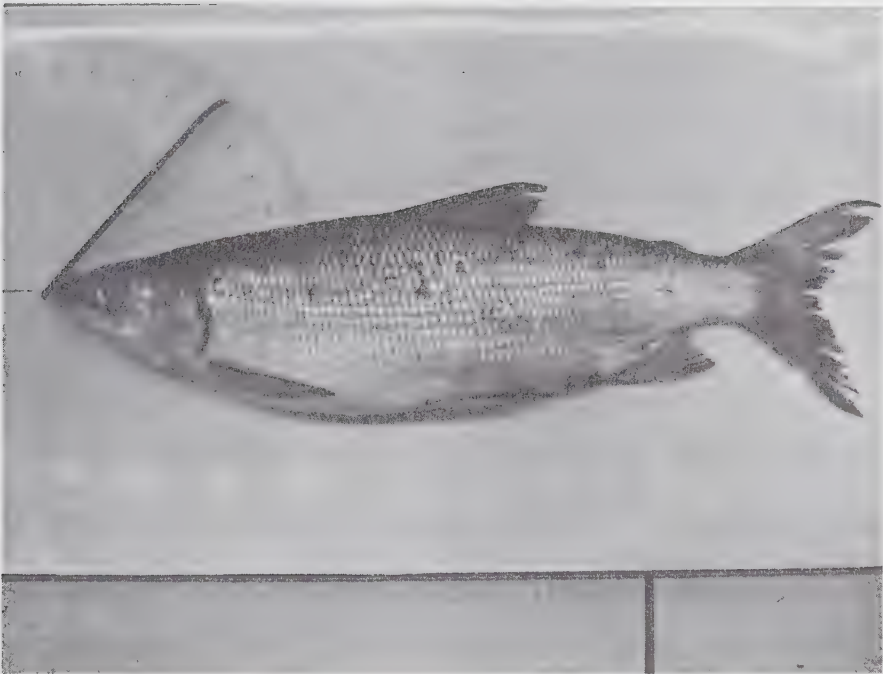
Body proportions and meristic counts were made on specimens which had been previously frozen to preserve them. The specimens were thawed in cold water and measured the same day. The condition of the fish was very similar to that of a fresh specimen. The one exception to this method was in the case of fish from Unnamed Lake which were preserved in a 10% formalin solution in the field because of the necessity of using a float-equipped light aircraft to obtain samples from this lake. All measurements and counts were made according to the method of Hubbs and Lagler (1958) except head lengths which in this study excluded the opercular membrane. Standard length was measured to the nearest millimeter using a meter rule. All other measurements were made with dial calipers read to the nearest 0.1 mm.

Of the 25 measurements and 11 meristic counts made on each specimen the following were considered most useful for the identification of individuals. (Unpaired t-test indicated that the means were highly significantly different ($P < 0.01$) between *C. clupearformis*, presumed and experimentally produced hybrids and *C. artedii*.)

- (a) Ratio of upper jaw length to length of base of adipose fin.
- (b) Ratio of mandible length to head length.
- (c) Ratio of standard length to head length.
- (d) Ratio of upper jaw length to head length.
- (e) Ratio of standard length to length of base of adipose fin.
- (f) Gill rakers. The number of gill rakers was counted under magnification on the dissected first left gill arch.
- (g) Angle of the premaxilla. This is the angle which the premaxilla makes with a horizontal line extending from the ventral extremity of the premaxilla to the fork of the caudal fin. A special measuring device (Figure 12) was constructed for this purpose.

The relative egg size of *C. artedii*, *C. clupearformis* and presumed wild hybrids was determined by placing individual eggs

FIGURE 12. Device used for measuring angle of premaxilla.



side by side for a distance of 500 mm., along a steel rule graduated in millimeters, and calculating the average egg diameter. All eggs were fertilized and water hardened for a period of 48 hours before measurement. This character was considered as a possible means of supporting the hybridization theory but was not combined with other characters for identification purposes.

C. Experimental Breeding and Rearing

Wild adult fish of both parental species as well as hybrids were used as parents for hybrid embryo mortality and rearing tests. Ripe adult fish were obtained by gill netting and upon removal from the nets were transferred to a container of lake water. Out of direct sunlight eggs were stripped from the females into a plastic bowl and sperm was immediately stripped on the eggs from ripe male fish. No water was added to the eggs and sperm but to ensure adequate mixing the bowl was moved gently in a circular motion for approximately 90 seconds. Lake water was then added to the mixture and the container was kept in motion for 15 minutes to prevent the eggs from clumping. The eggs were then rinsed in lake water several times to get rid of excess seminal fluid and transferred to jars filled with lake water. When the spawn taking operation was completed the jars were transferred to a container of ice water and transported within 24 to 36 hour periods to a fish hatchery or a laboratory.

Incubation was carried out at the Raven trout rearing station by placing the eggs in 125 ml. Erlenmeyer flasks and maintaining a flow of spring water at 4°C through the flasks just sufficient to keep the eggs moving slowly. The building in which the flasks were housed was kept dark throughout the incubation period.

In the laboratory, the eggs were placed in trays with plastic sides and nylon screen bottoms. Forty cc. (settled volume) of eggs were placed in each tray so that they formed a single layer over 75% of the bottom of the tray. The trays were immersed in a temperature controlled fiberglass "Living Stream" recirculation tank containing Wabamun Lake water. The temperature of the water in the recirculation tank was not rigidly controlled during the 1969-70 incubation trials. It varied from a minimum of 2.0°C to a maximum of 4.0°C over the incubation period. In the 1970-71 trials the incubation water temperature was controlled at $4^{\circ}\text{C} \pm 0.04$ and in the 1971 trials at $2^{\circ}\text{C} \pm 0.5$. An open pore foam rubber filter for removal of solid wastes and an activated charcoal filter for removal of nitrogenous wastes were installed at one end of the recirculation tank. The eggs were treated periodically with malachite green (conc. 0.5 ppm.) to control fungus and white - spot disease. A cover was placed over the tank so that the eggs were not exposed to natural or artificial light.

In the 1969-70 trials after 80 days of incubation, it was noticed that the tray covers had warped slightly and there was a risk of exchange of eggs from one tray to another. The eggs were transferred to 1 gallon jars fitted with screen tops, totally immersed in the tank for a period of two days while the tray covers were being improved. This change in incubation method proved to be costly as very large die-offs of the eggs occurred before they could be restored to the trays. The die-off was presumed to be due to insufficient circulation in the jars. Although a more than adequate number of eggs of each lot to continue the trials survived the die-off, it was not possible to count the number of eggs lost because of rapid deterioration of the egg membranes. The unknown loss was calculated by subtracting the known mortality plus the number hatched from the number of eggs started. The number of eggs at the start was estimated for both parental species by determining the number in a settled volume of 40 cc. and there is undoubtedly an error involved.

Progeny from the artificial breeding of the pure parental types, the heterospecific crosses and the back crosses were reared in the laboratory in aquaria and in the temperature controlled 'Living Stream' tank. Individual lots of each cross were pooled for the rearing experiments due to space limitations. They were fed on brine shrimp nauplii (*Artemia*) until they reached a length

of approximately 25 mm. at which time the diet was changed to frozen adult brine shrimp.

It was anticipated that it would be very difficult to rear young whitefishes in the laboratory (Svardson pers. comm.), hence, fry from each pooled lot were transferred to separate borrow pits located west and north of Edmonton. As far as could be determined, these ponds contained no native fish species prior to the introduction of the experimental fish. The young fish placed in ponds utilized only the natural food available to them. Samples were removed as required by seine nets and/or monofilament gill nets. The pond populations were utilized for morphological and biochemical analysis rather than laboratory reared individuals since the growth of the former far exceeded that of the latter.

D. Electrophoretic Studies

Electrophoretic studies have been employed by many workers in the past decade to assist in the identification of species and as a tool to establish phylogenetic relationships (Tsyuki et al. 1965, and Tsyuki et al. 1968). They have also been used to assist in identification of hybrids (Tsyuki and Roberts 1965, Aspinwall and Tsyuki 1968, Stewart MS 1966, Koehn MS 1967). Electrophoretic analysis of muscle myogens have shown them to be species specific and virtually unaffected by factors other than genetics (Tsyuki and Roberts 1966).

For this reason and because of the relative ease of obtaining, preserving and storing samples, muscle was chosen as the component for electrophoretic analysis in this study.

Electrophoresis of blood serum proteins was also attempted but the success in analyzing these proteins was considerably less than that achieved in muscle proteins especially when using stored, frozen samples, so this technique was abandoned.

Muscle samples were taken from the right side of the fish posterior to the dorsal fin and above the lateral line (the left side was left intact for other morphological studies). Samples were taken immediately after the fish was killed and the sample was then placed in a glass vial, labelled as to location, date and specimen number, and placed on dry ice. After transportation to the laboratory on dry ice the samples were stored in a freezer chest at -10°C until electrophoresis was carried out.

Starch-gel electrophoresis was carried out on muscle samples of coregonines from nine of the study lakes as well as on the progeny of the artificial breeding experiments. The following method was employed. Samples of muscle were homogenized in phosphate buffer 0.055M, pH 8.5. The ratio of muscle to buffer was 1:2. The homogenate was then centrifuged for 15 minutes at $5000 \times g$ and the supernatant collected. Electrophoresis was

conducted on the supernatant for 4 hours at 400v and at a temperature of 20° C. Protein zones were stained with amido black. Photographs were taken of various gels before deterioration of the gel or protein resolution occurred.

E. Food Habit Studies

Many of the specimens taken during this work were captured during or close to the spawning period. Cisco stomachs contained little or no food material and lake whitefish stomachs were either empty or contained varying amounts of a single food item - whitefish eggs. Few hybrids were taken during this period so that diet comparisons between the three groups were not meaningful.

Analysis of the stomach contents of a sample of lake whitefish, ciscoes and hybrids taken in Utikuma Lake in June, 1971, provides the only useful basis for diet comparisons obtained during this study.

The fish were taken mainly in overnight gill net sets although some specimens were obtained by lifting the nets during the day. Fish from both types of net sets were pooled for food studies as were the sexes. All fish were frozen until such time as stomach analyses could be made. No attempt was made to stop digestion after death of the fish by injection of preservative into the stomach.

The method of analyzing the stomach contents was similar to that described by Thompson (1959). A stomach was allotted points from zero to 20 according to fullness; a zero value being assigned to an empty stomach, and a value of 20 to a full stomach. An intermediate degree of fullness was assigned a value between zero and 20. Stomach contents were then examined and food items were identified. The percentage of the volume of the stomach contents contributed by each food item was estimated.

F. Age - Growth Studies

A comparison of the growth of lake whitefish, hybrids and ciscoes was made using fish from Utikuma Lake, North Buck Lake and Wolf Lake. The ages of the fish were determined by the scale reading method. Scales were removed from the right side of the specimens, approximately halfway between the origin of the dorsal fin and the lateral line. Several good scales were chosen from the sample and impression of these were made on soft plastic using a jeweller's press. The scale impressions were examined by projecting the scale image onto a white surface with a Bausch and Lomb microprojector which provided a magnification of 40 diameters. Scales which were difficult to interpret were also examined with an Eberbach projector which provided magnification of 65 diameters. All scales were read by a

technical assistant and subsequently read by the author. Generally good agreement in aging the fish was obtained but in cases of disagreement the age as determined by the author was used.

RESULTS

A. Morphological Analysis of Wild Adults

1. Gill rakers. Svardson (1965) stated that gill rakers are of the utmost importance in studying different whitefish forms since they are the only morphological character so far proved not to be considerably modified by environment. In support of this he points out that the genetical basis of their number is proved by transplantations, artificial selection experiments and their intermediate number in species hybrids. Other authors including Lindsey (1962), Koelz (1929), Fenderson (1964), Hubbs and Lagler (1958), and Scott and Smith (1962) also give the number of gill rakers prominence as a distinguishing feature in whitefishes. In view of this evidence, the number of gill rakers in the parent species and hybrids received emphasis in the present study. Figures 13 - 20 show first branchial arch gill raker distribution in coregonines from the ten lakes included in the study. As previously noted *C. clupeaformis* and *C. artedii* are sympatric in seven of the

FIGURE 13. Gill raker distribution of selected samples of coregonines from Wolf Lake.

FIGURE 14. Gill raker distribution of selected samples of coregonines from Utikuma Lake.

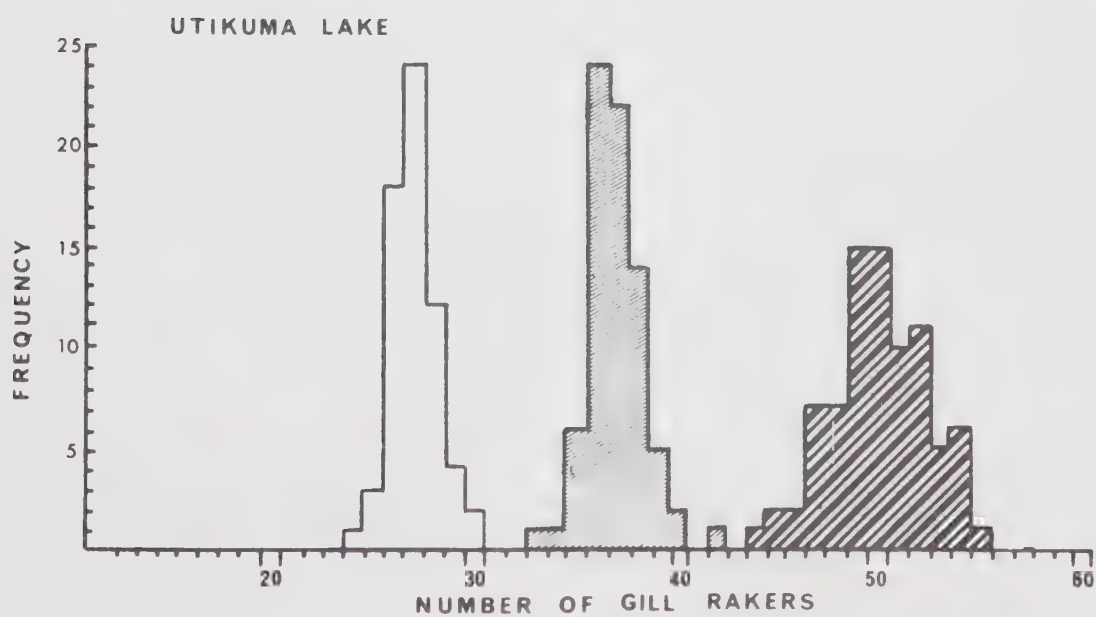


FIGURE 15. Gill raker distribution of selected samples of coregonines from Cold Lake. .

FIGURE 16. Gill raker distribution of selected samples of coregonines from Unnamed Lake.

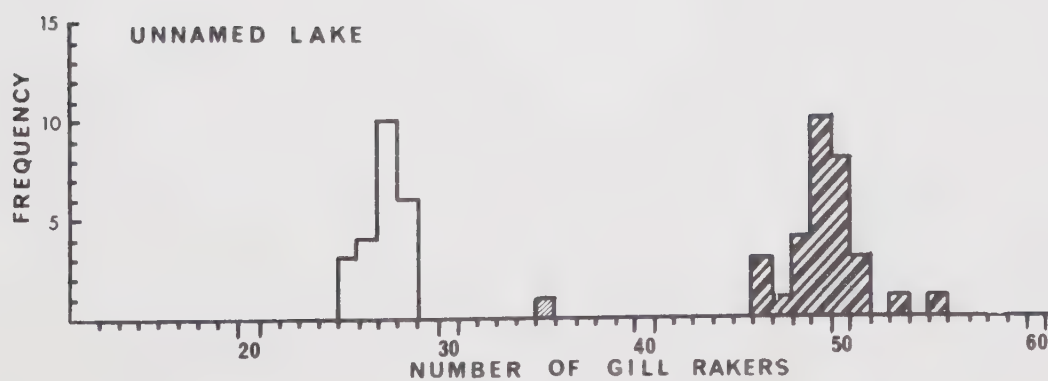
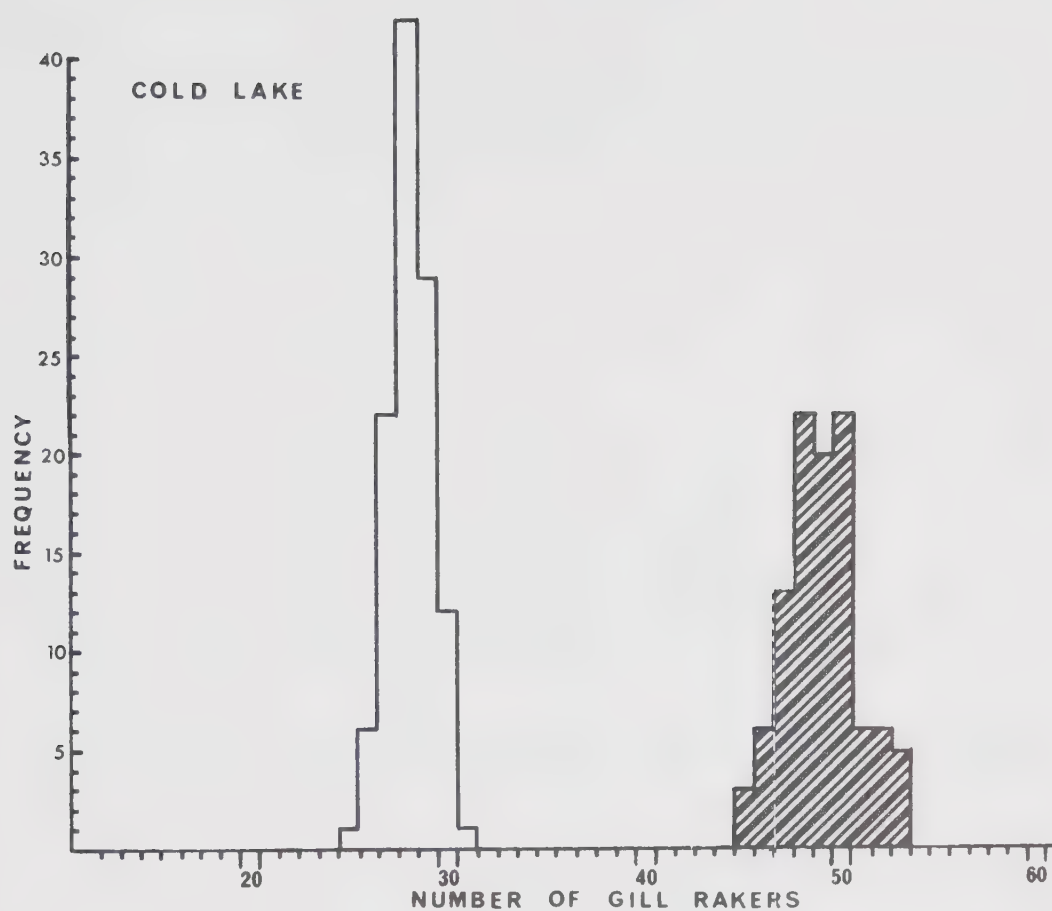


FIGURE 17. Gill raker distribution of selected samples of coregonines from North Buck Lake.

FIGURE 18. Gill raker distribution of sample of coregonines from Square Lake.

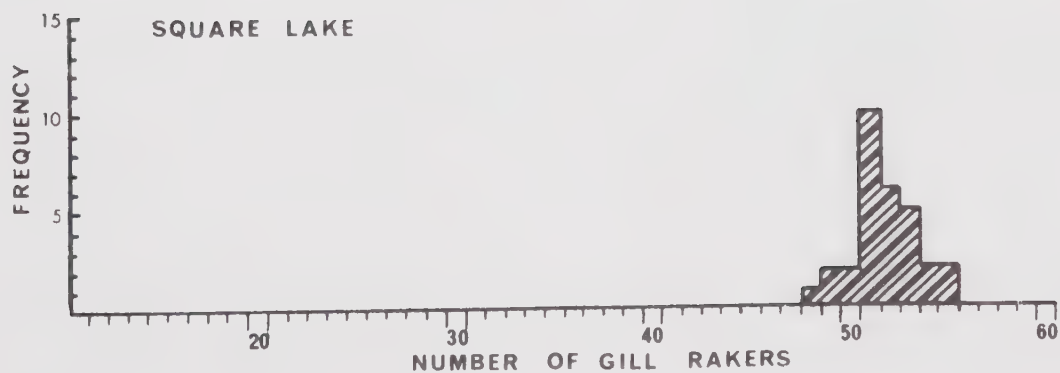
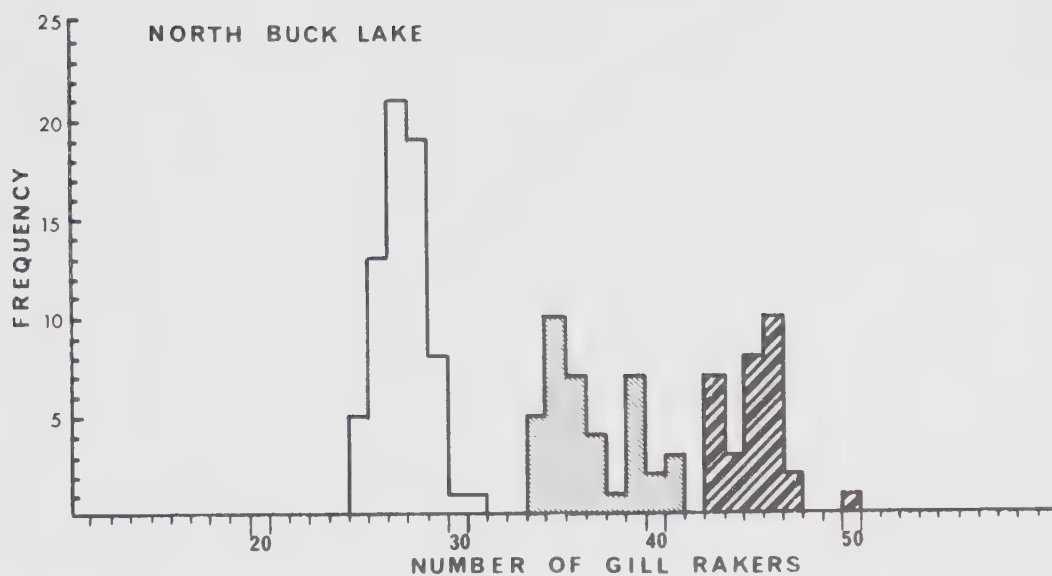


FIGURE 19. Gill raker distribution of selected samples of coregonines from Touchwood Lake.

LAKE
WHITEFISH

CISCO

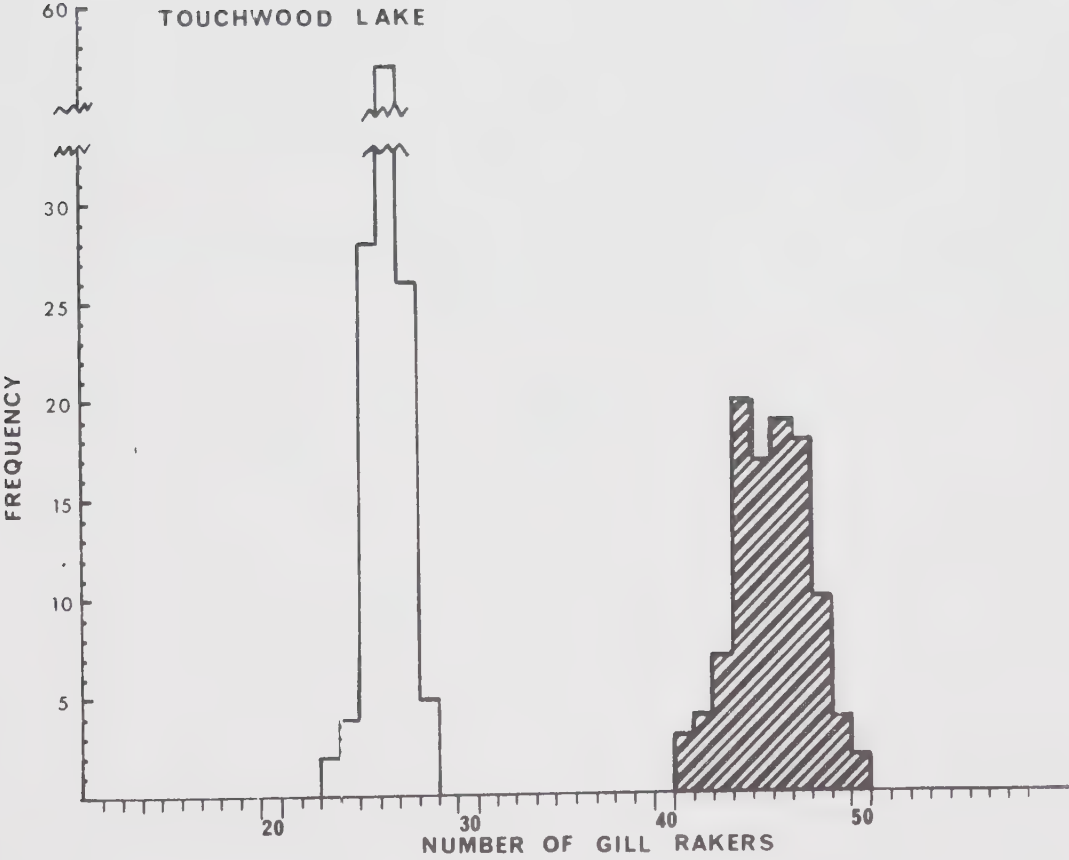
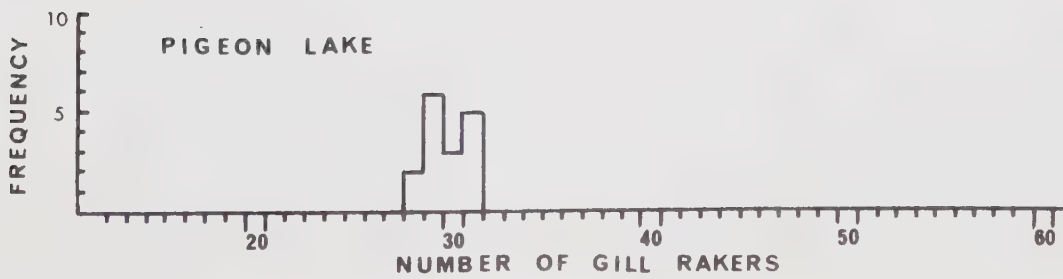


FIGURE 20. Gill raker distribution of selected samples of coregonines from Nipisi Lake.

FIGURE 21. Gill raker distribution of sample of coregonines from Pigeon Lake.



lakes, *C. artedii* is allopatric in two lakes and *C. clupeaformis* allopatric in one. For the purpose of gill raker information only, the count of one additional allopatric population, that of Pigeon Lake is included (Figure 21).

It is apparent in Figure 22 that, on the basis of gill raker number, a single population of whitefish with a low count exists in Pigeon Lake and also in Smoke Lake, and that single populations of high count fish exist in Square and Kehiwin Lakes. Cold Lake and Touchwood Lake each have populations of both high and low count forms. In Utikuma Lake, North Buck Lake, Nipisi Lake, Wolf Lake and Unnamed Lake, populations of both low and high count forms and an intermediate form, presumed to consist chiefly of F_1 hybrids, are present. It is further evident in the latter group of lakes that definite separation between low count populations and that of intermediates exists. This could be indicative that backcrossing between hybrids and low count forms is not taking place or is so rare as not to be reflected in the samples. On the other hand, the separation between intermediates and high count forms is not as obvious. This could be taken as evidence that either some backcrossing between hybrids and the high count form is taking place or simply that the range of gill raker numbers in hybrids overlaps that of the high count form.

The low count forms in all lakes studied represent specimens of *C. clupeaformis* while the high count forms represent *C. artedii* (or individuals of the *C. artedii* 'complex'). This identification is in general agreement with various workers who have examined northwestern Canadian whitefishes, (Dymond 1943, 1947; Hubbs and Lagler 1958; Scott and Crossman 1969; Lindsey 1962, 1963). Koelz (1929) gives the range of 1st arch gill raker number for *C. artedii* in Lake Michigan as 46-50 with extremes of 41 and 55, for Lake Huron as 45-50 with extremes of 40 and 53 and for Lake Erie as 44-48 with extremes of 41 and 53. This also is in close agreement with counts obtained in this study. Many writers have referred to the great variability in coregonines and particularly to the cisco group. This is borne out in Figure 22 which shows the variation in range and means of gill raker numbers of the cisco populations from the study lakes. The variability of *C. clupeaformis* appears to be less marked than that of *C. artedii*.

Differences in the actual appearance of the first arch gill rakers may be noted by examining Figure 23.

2. Premaxillary Angle

The principal method used by fishermen for identifying presumed hybrids is by their so called 'blunt snout'. Koelz (1929) describes a specimen of what he considered to be a hybrid between

FIGURE 22. Comparison of numbers of gill rakers of coregonines from 10 study lakes. Range is shown by the horizontal line; the mean by the longest vertical line. The black part of each bar comprises 2 standard errors on either side of the mean. The black part plus white bar at either end outline one standard deviation on either side of the mean.

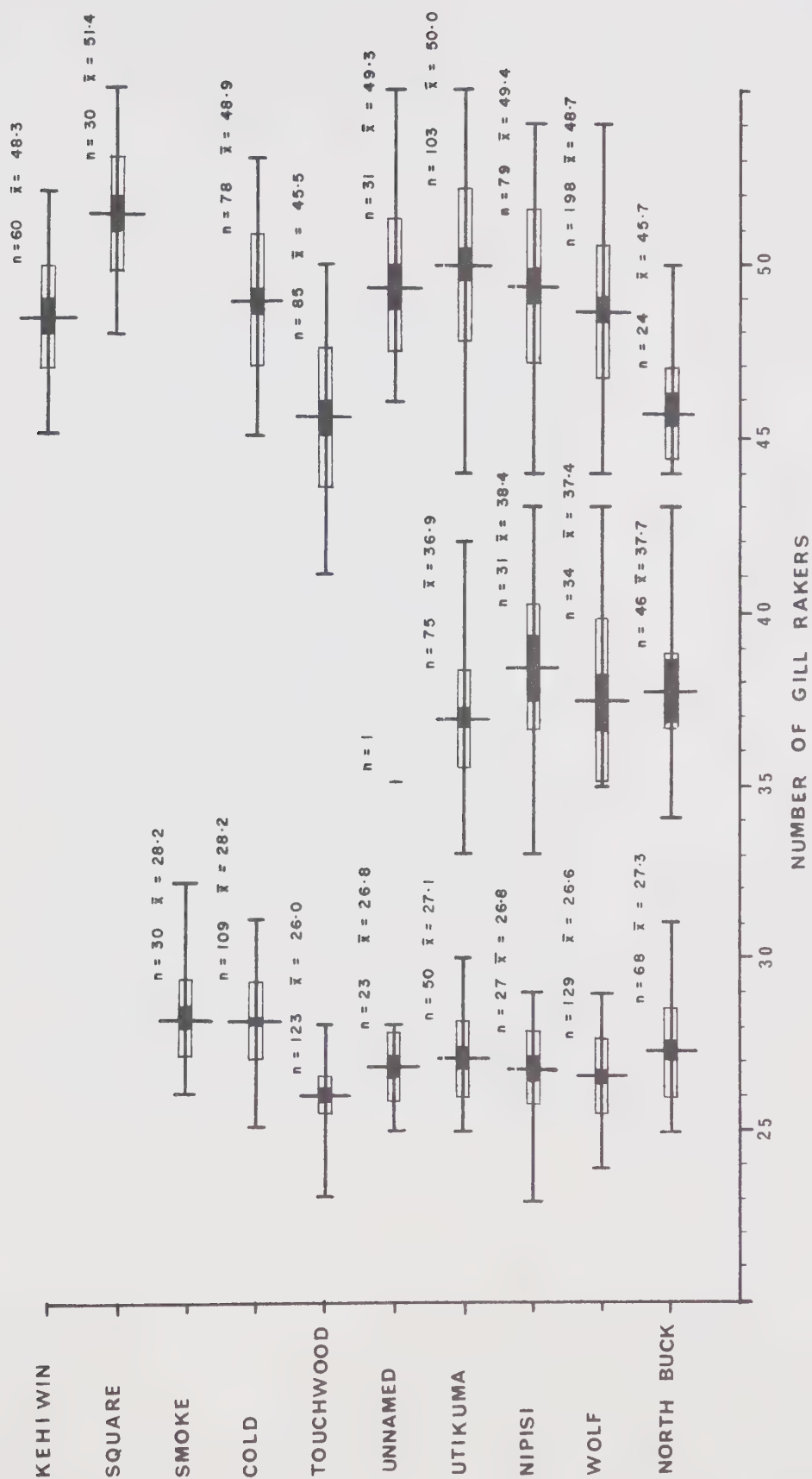
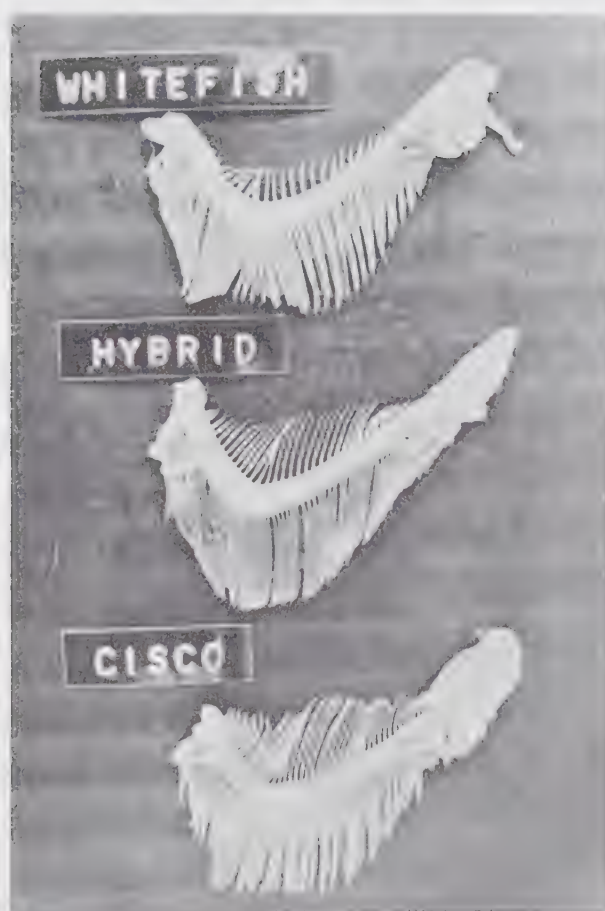


FIGURE 23. Photograph showing 1st arch gill rakers of lake whitefish, cisco and presumed hybrid. (Utikuma Lake samples.)



C. clupeaformis and *C. artedii* as having the premaxillaries bent at an angle of little more than 90° . Gasowska (1958) refers to the hybrid of *C. lavaretus maraenoides* Polyakov x *C. albula* as being quite variable in mouth shape but more closely resembling the female parent. Since it is generally accepted that the premaxillaries of *C. clupeaformis* are retrorse in position, while those of *C. artedii* are antrorse in position, it was felt that the position of the premaxillaries in the hybrids may be a useful character in distinguishing hybrids from the parent species.

The results obtained by measuring the angle of the premaxillaries in relation to the horizontal axis of the body are presented in Table 1.

The data in Table 1 indicate that there is complete separation between *C. clupeaformis* and *C. artedii* in all lakes. The presumed hybrids tend to overlap more with *C. clupeaformis* in this character than they do with *C. artedii* although in the case of North Buck Lake there is an obvious overlap with ciscoes and in the case of Nipisi Lake and Wolf Lake, a slight overlap. The mean angle size of hybrids in all lakes is also nearer to that of lake whitefish than to cisco, being near 90° although not greater than 100° , except in one extreme individual from Nipisi Lake. It is of interest to note that the gill raker number in hybrids from North Buck Lake is skewed towards that

TABLE 1. Premaxillary angle of *C. clupearformis*, *C. artemidi* and presumed hybrids in ten study lakes (numbers in parentheses indicate sample size).

LAKE	<i>C. clupearformis</i>		HYBRIDS		<i>C. artemidi</i>	
	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN
KEHIWIN					(57) 34-51	41.6
SQUARE					(30) 28-48	39.9
SMOKE	(30) 90-113	102.3				
COLD	(11) 95-127	110.6			(80) 29-50	41.4
TOUCHWOOD	(74) 90-114	103.4			(106) 25-69	43.1
UNNAMED	(8) 108-115	110.7	(1) 93	93	(7) 38-58	49.8
UTIKUMA	(62) 84-117	110.1	(38) 74-98	84.3	(80) 33-65	46.5
NIPISI	(26) 91-112	103.7	(27) 68-111	82.3	(73) 31-69	48.4
WOLF	(52) 91-115	98.7	(35) 53-98	83.40	(99) 28-64	44.2
N. BUCK	(65) 83-111	99.0	(21) 50-91	73.1	(24) 38-66	51.3

of ciscoes and there is also a greater overlap in premaxillary angle between these two groups in this lake. This may be suggestive of backcrossing. In field examination of North Buck Lake populations there are also more doubtful individuals, i.e. as to whether they are hybrids or ciscoes.

It should be noted that the premaxillary angle of some individuals of *C. clupeaformis* is less than 90° in Utikuma and North Buck Lakes. This is not in agreement with the observations of Koelz (1929) on lake whitefish in the Great Lakes. He states that "the premaxillaries are in retrorse position." and again in describing lake whitefish reared in the New York Aquarium states: "The premaxillaries are often vertical in position which is not known to be the case in normally reared individuals."

In most lakes where hybrids were found in this study the near-vertical position of the premaxillaries does give the snout the 'blunt' appearance used by fishermen to identify 't-whites' as they have named them in Alberta, and in fact our experience indicates that it is possible to identify most hybrids by this character. The degree of overlap with both parents however precludes positive identification by examining the position of the premaxillaries.

Figure 24 shows the more common position of the premaxillaries of the cisco, hybrid and lake whitefish as found in this study.

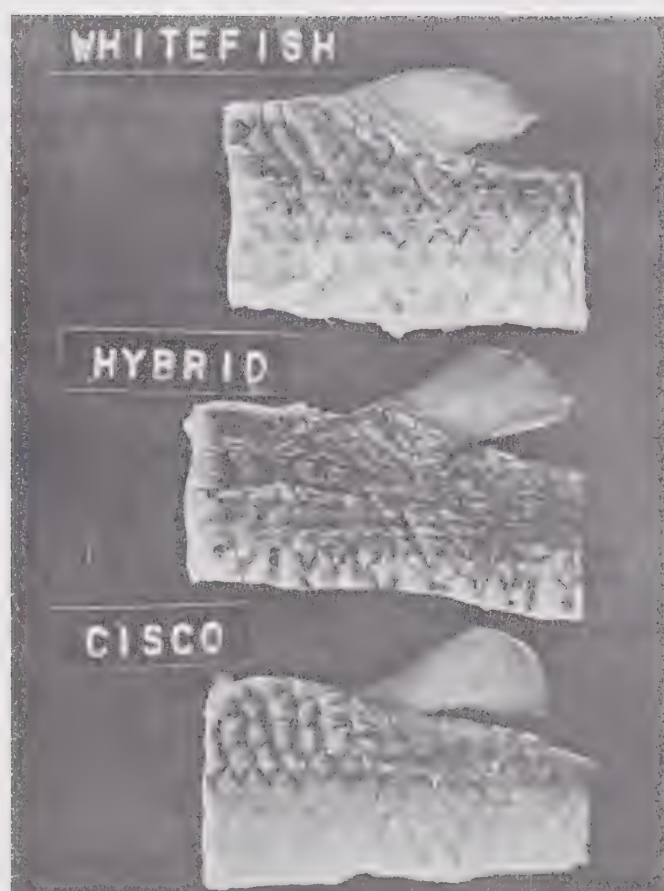
FIGURE 24. Photograph showing differences between premaxillary angle of cisco (upper), presumed hybrid (middle) and lake whitefish (lower). Wolf Lake samples.



3. Ratio of Standard Length to Length of Base of Adipose Fin

In stating that the size of the adipose is extremely variable and has little value as a systematic character, Koelz (1929) refers to the length of the fin. In examination of my specimens it became obvious that the base of the fin, i.e. its attachment to the body, appeared quite different in the two parental species. *C. clupearformis* has a long base while in *C. artedii* the fin is more club-like in appearance with a short or narrow base. The presumed hybrids show an intermediate type of base. Differences between the three groups are illustrated in Figure 25. The ratio of the standard length to the length of the base of adipose fin was calculated on samples from the populations in each lake. Using the statistic "t" to test the significance of difference of means of these ratios, it was found that the differences were highly significant ($P < .01$) between ciscoes and lake whitefish and between hybrids and parents in each lake where hybrids were found. Although there was no overlap between lake whitefish and ciscoes or between hybrids and lake whitefish, some overlap of cisco and hybrid individuals does exist. One cannot therefore discriminate between individuals of the latter groups by this character alone.

FIGURE 25. Photograph showing differences in length of base of adipose fin in lake whitefish, cisco and presumed hybrid (Utikuma Lake samples)



4. Ratio of Upper Jaw Length to Length of Base of Adipose

It is generally considered that ciscoes because of their wider gape have a longer maxillary in relation to the head than lake whitefish. The means of this ratio (t-test) however did not prove to be significantly different between ciscoes and hybrids in some lakes. The ratio of upper jaw length to length of adipose fin base was considered to give more reliable separation. Sample plots of this ratio against gill raker number are shown for Utikuma Lake fish (Figure 26), Touchwood Lake fish (Figure 27), Wolf Lake fish (Figure 28) and Nipisi Lake fish (Figure 29). Graphical inspection indicates complete separation of the two species in the four lakes but there are overlap tendencies between hybrids and ciscoes in Wolf Lake and Nipisi Lake. Identification of some individuals by this method is therefore not positive.

5. Ratio of Head Length to Standard Length

As previously indicated, this ratio appeared to be useful in assisting in discriminating between the three groups but considerable overlap between individuals was observed.

6. Ratio of Head Length to Length of Mandible

Again, due to overlap in this ratio between lake whitefish, hybrids and ciscoes, this character was not effective by itself in separating certain individuals of one group from those of another.

FIGURE 26. Discrimination between lake whitefish, cisco and hybrids in Utikuma Lake on basis of gill raker number and ratio of upper jaw length to length of base of adipose fin.

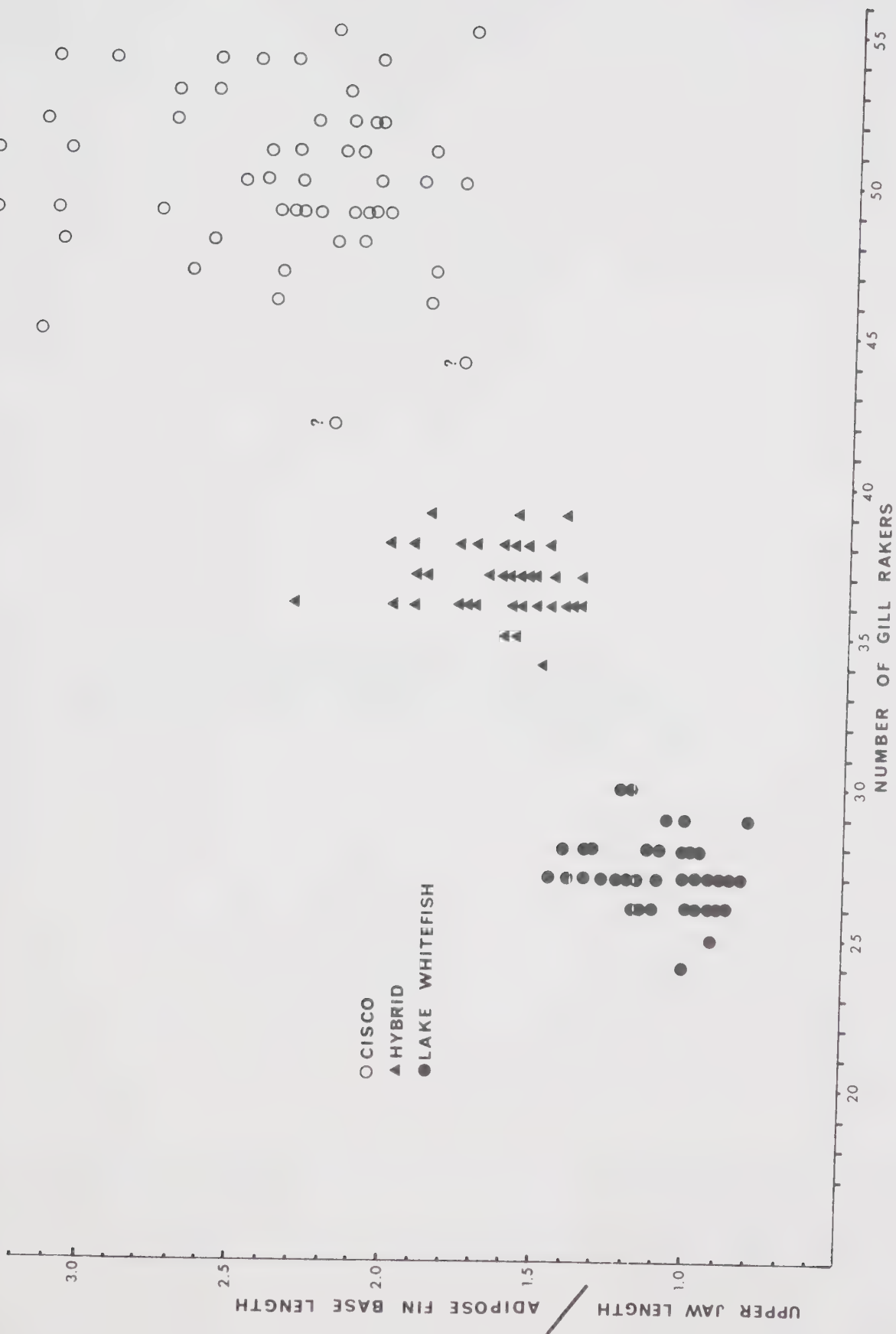


FIGURE 27. Discrimination between sympatric lake whitefish and cisco in Touchwood Lake on basis of gill raker number and ratio of upper jaw length to length of base of adipose fin.

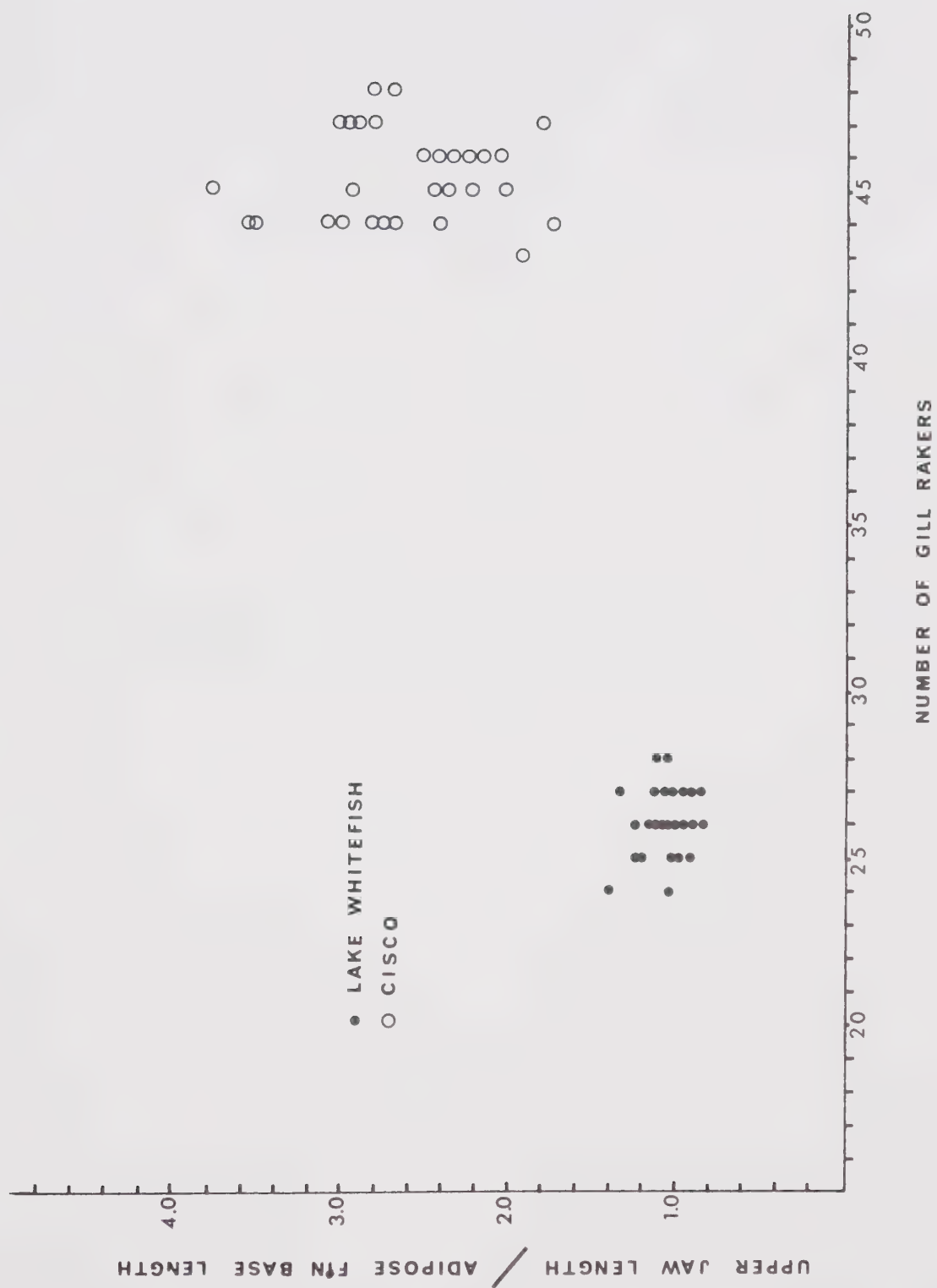


FIGURE 28. Discrimination between lake whitefish, cisco and hybrids in Wolf Lake, on basis of gill raker number and ratio of upper jaw length to length of base of adipose fin.

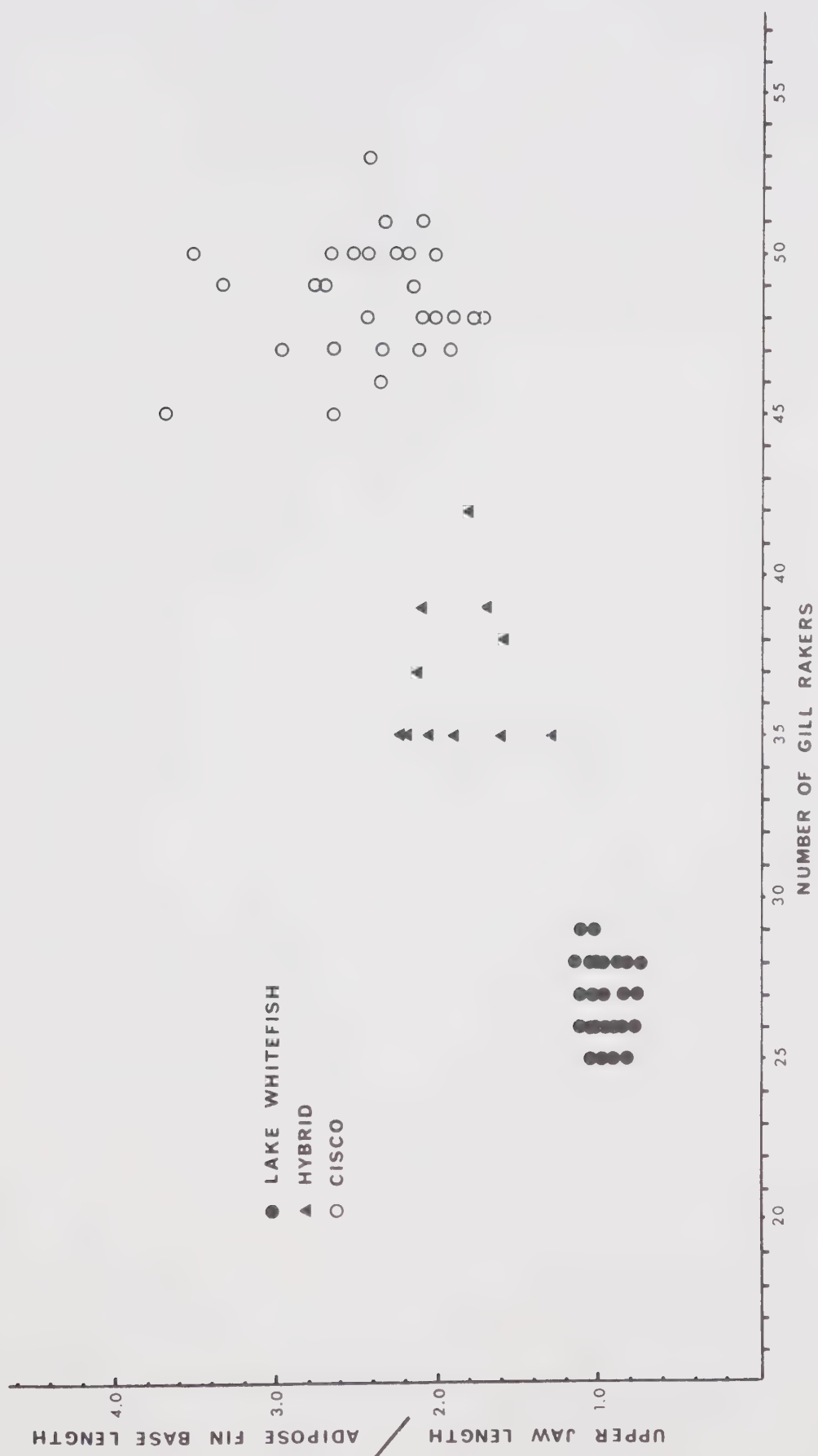
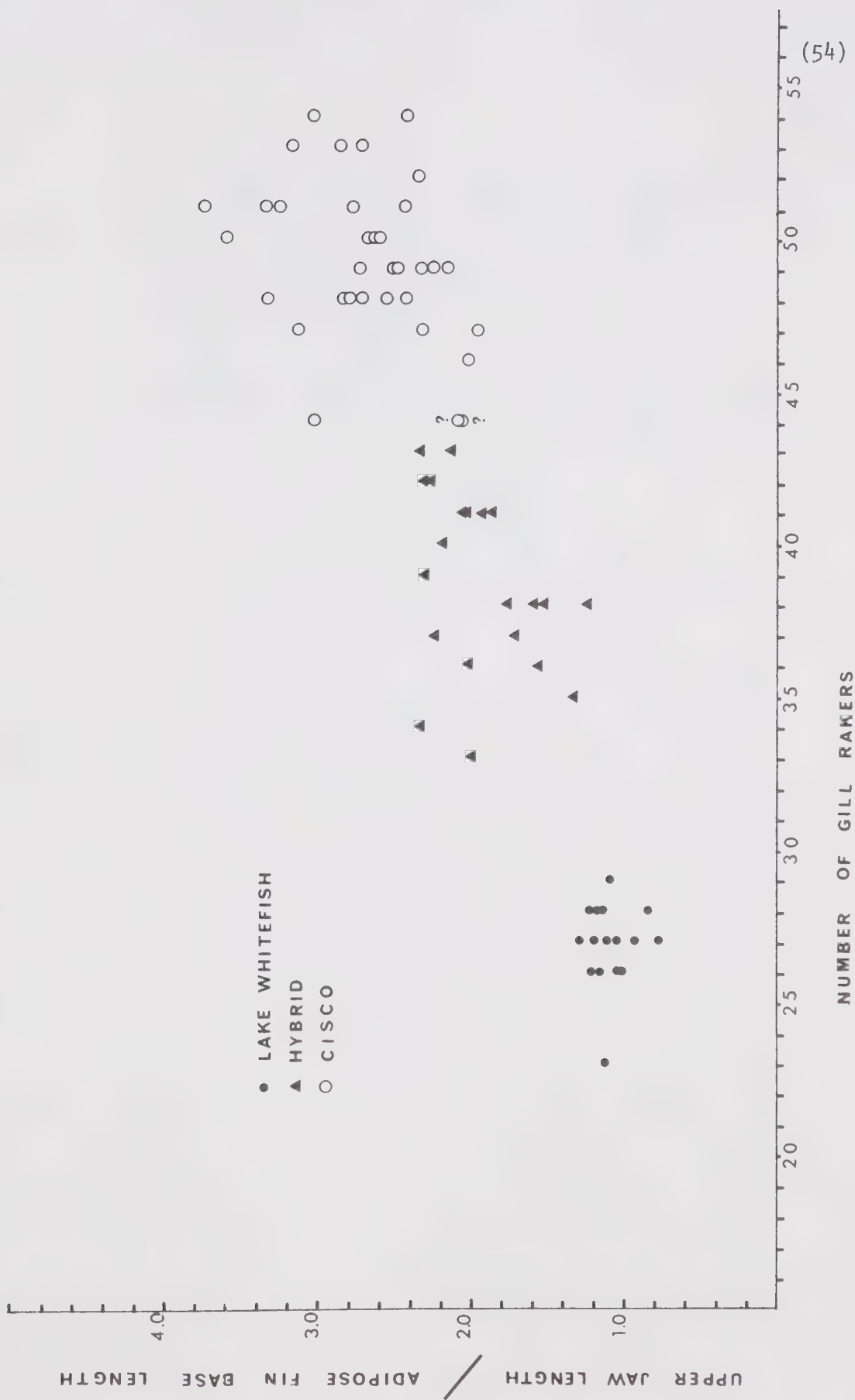


FIGURE 29. Discrimination between lake whitefish, cisco and hybrids in Nipisi Lake on basis of gill raker number and ratio of upper jaw length to length of base of adipose fin.



Since no single character of those tested was completely reliable for identification of hybrids, methods of combining characters to enhance separation between hybrids and whitefish, and hybrids and ciscoes were explored. These methods were:

- (a) plotting premaxillary angle against gill raker number, and
- (b) construction of a simple character index which would combine the discriminating powers of several characters.

Results of plotting premaxillary angle against gill raker number using samples from Utikuma Lake, Nipisi Lake and Wolf Lake are shown in Figures 30, 31 and 32 respectively. As previously noted the premaxillary angle of hybrids more closely resembles that of whitefish than ciscoes. Gill raker counts of hybrids on the other hand tend to nearly overlap that of ciscoes while maintaining a distinct separation from the counts in lake whitefish. Figures 30 to 32 show that the plots of these two characters are useful in identifying hybrids. In the case of Nipisi Lake however, two individuals had gill raker counts of 44. One of these had been originally classed as a hybrid while the other had been identified as a cisco. Both individuals appear in the hybrid group in Figure 31 which suggests that the original identification of one of them as a cisco, was incorrect. It is possible, however, that this individual could be a cisco with an unusually high premaxillary value. Three individuals classed as hybrids in the Wolf Lake sample are also somewhat removed from

FIGURE 30. Discrimination between lake whitefish, cisco and hybrids in Utikuma Lake on basis of gill raker number and premaxillary angle.

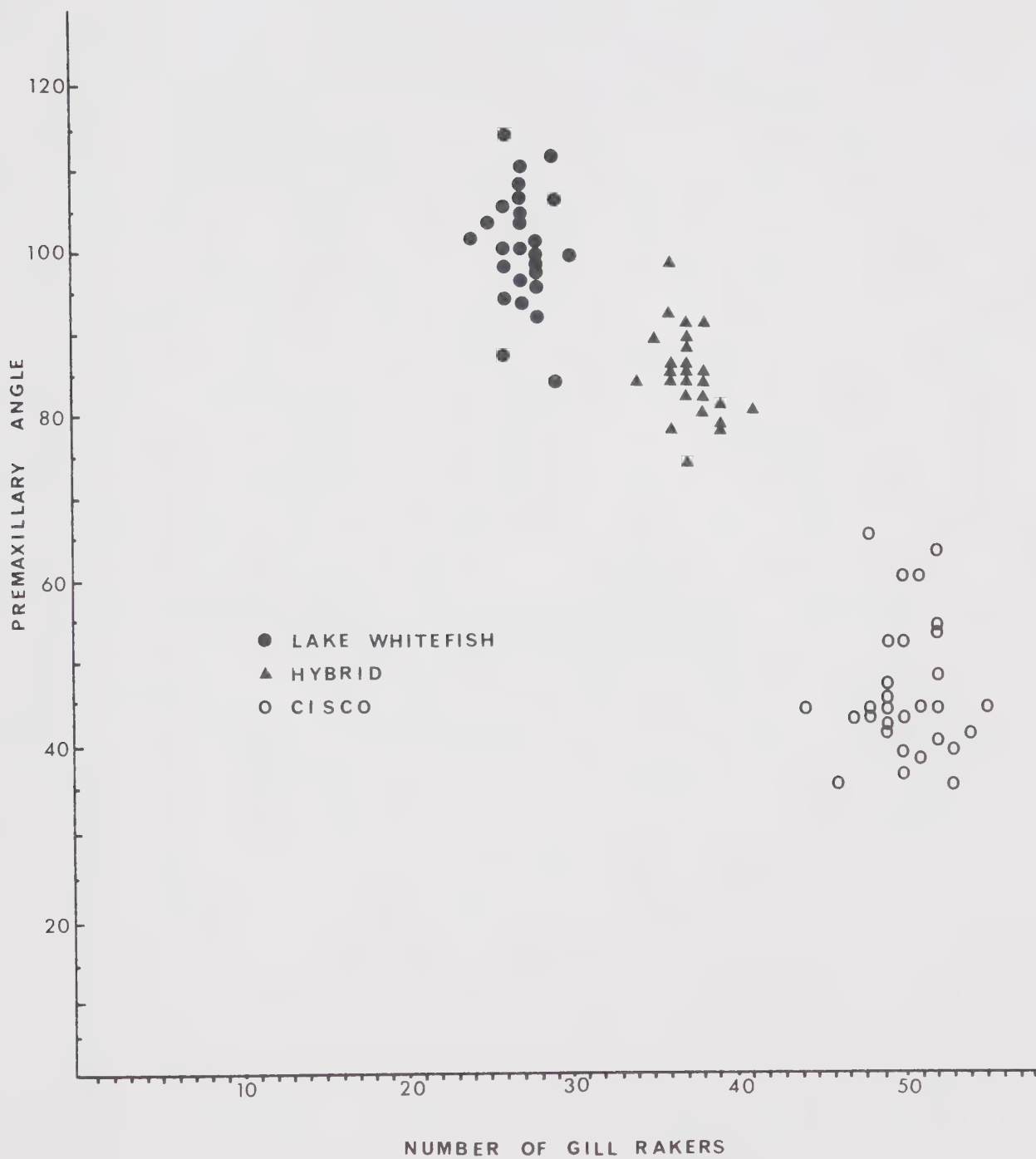


FIGURE 31. Discrimination between lake whitefish, cisco and hybrids in Nipisi Lake on basis of gill raker number and premaxillary angle.

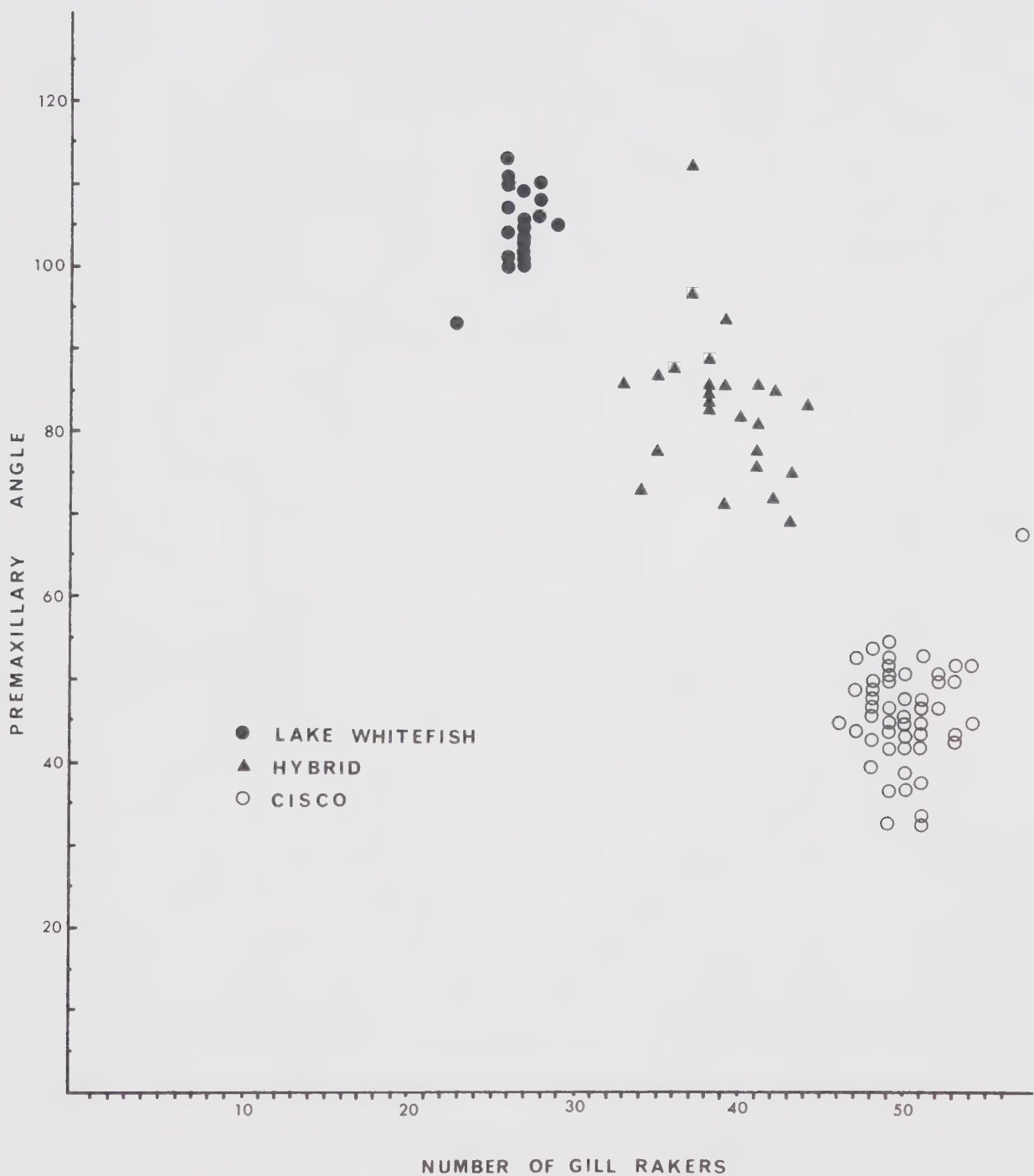
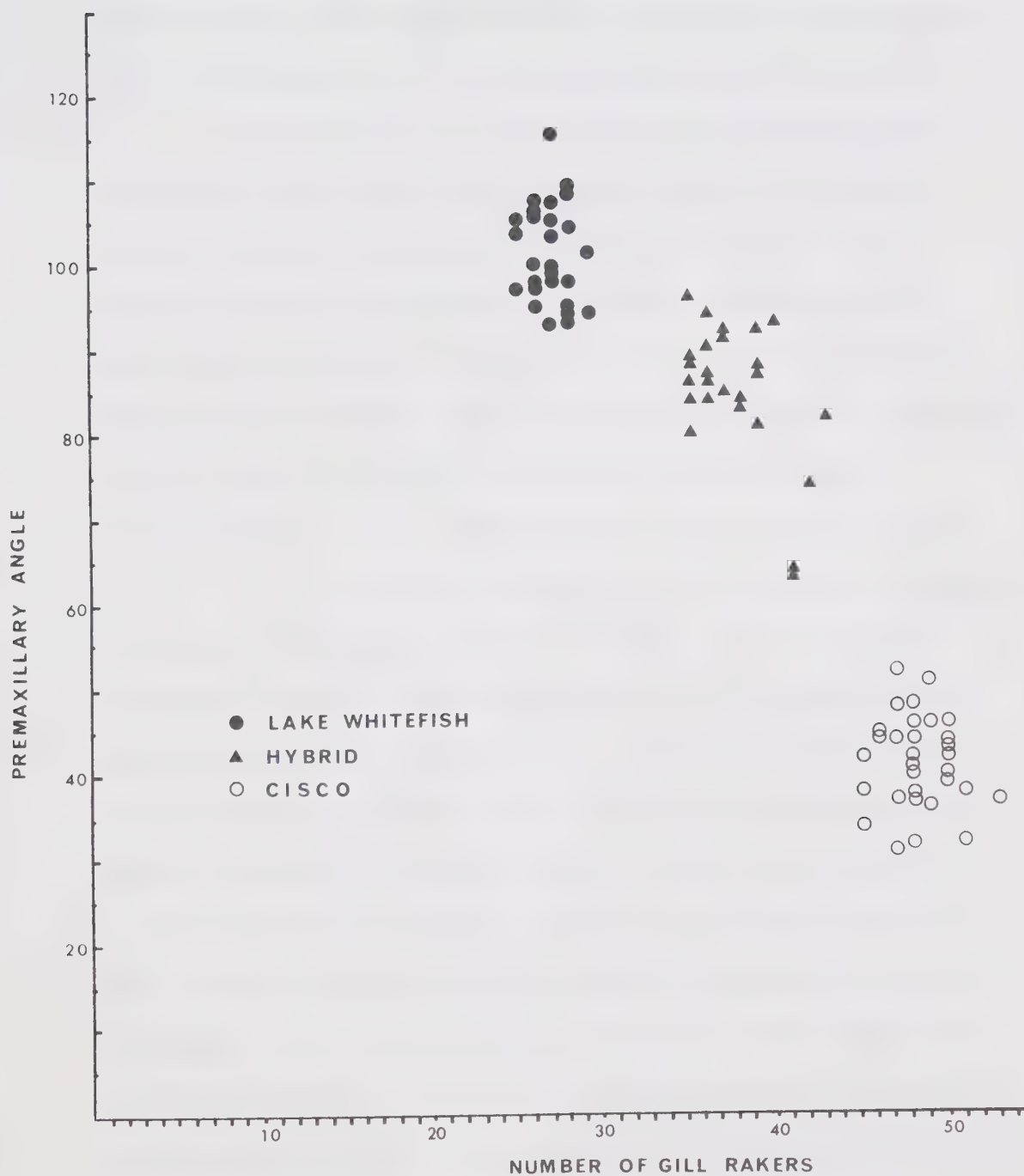


FIGURE 32. Discrimination between lake whitefish, cisco and hybrids in Wolf Lake on basis of gill raker number and premaxillary angle.



the group which may create some doubt as to their positive identification. The method supports the original identification of all individuals in the case of Utikuma Lake (Figure 30).

Construction of a character index was based on four characters, namely, gill raker number, premaxillary angle, ratio of standard length to adipose base and ratio of head length to length of mandible. The three latter characters were found by graphical inspection to have a low correlation with gill raker number, hence in looking for support (independent of gill rakers) that the three forms are morphologically distinguishable, these three characters were considered valid.

Another source of possible error in attempts to separate the forms when using ratios of body parts is the problem of allometric growth. Since the samples of wild fish were almost entirely adult fish there was not a sufficiently wide range of sizes in each of the three forms to be able to determine satisfactorily whether there was allometric growth of the head in relation to standard length. The ratio of standard length to head length (initially considered useful) was therefore not used in calculating the character index. Allometric growth could also introduce a source of error in the ratios, standard length to adipose base and head length to length of mandible, but in the latter case there was sufficient overlap in head length and length of mandible in the three forms from Utikuma Lake to

demonstrate that allometric growth was not a significant source of error (Figure 33). It was considered that this would also hold true for the three forms in other lakes.

Since there was not, however, a sufficient number of individuals of the three forms with comparable standard length to demonstrate whether allometric growth would create a source of error in the use of the standard length to adipose base ratio, this potential source of error remains. Figure 34 shows the plot of adipose base length against standard length for the samples of lake whitefish, hybrids and ciscoes from Utikuma Lake.

In constructing the character index the total range for each character for lake whitefish and ciscoes combined is divided into 10 equal divisions. A score of 0.5 to 9.5 is assigned to each of the four characters with 0.5 chosen to include the extreme decile values for *C. clupearformis* and with 9.5 for the extreme decile values for *C. artedii*. The combination of these four characters into an index gives good separation between *C. clupearformis* and *C. artedii* in samples from the three lakes to which the index was applied. This is shown in Figures 35, 36 and 37 for Utikuma Lake, Nipisi Lake and Wolf Lake respectively. The hybrids (as shown by morphological intermediacy) from Utikuma Lake and Wolf Lake are also distinctly separated

FIGURE 33. Relationship between mandible length and head length in lake whitefish, cisco and hybrids from Utikuma Lake.

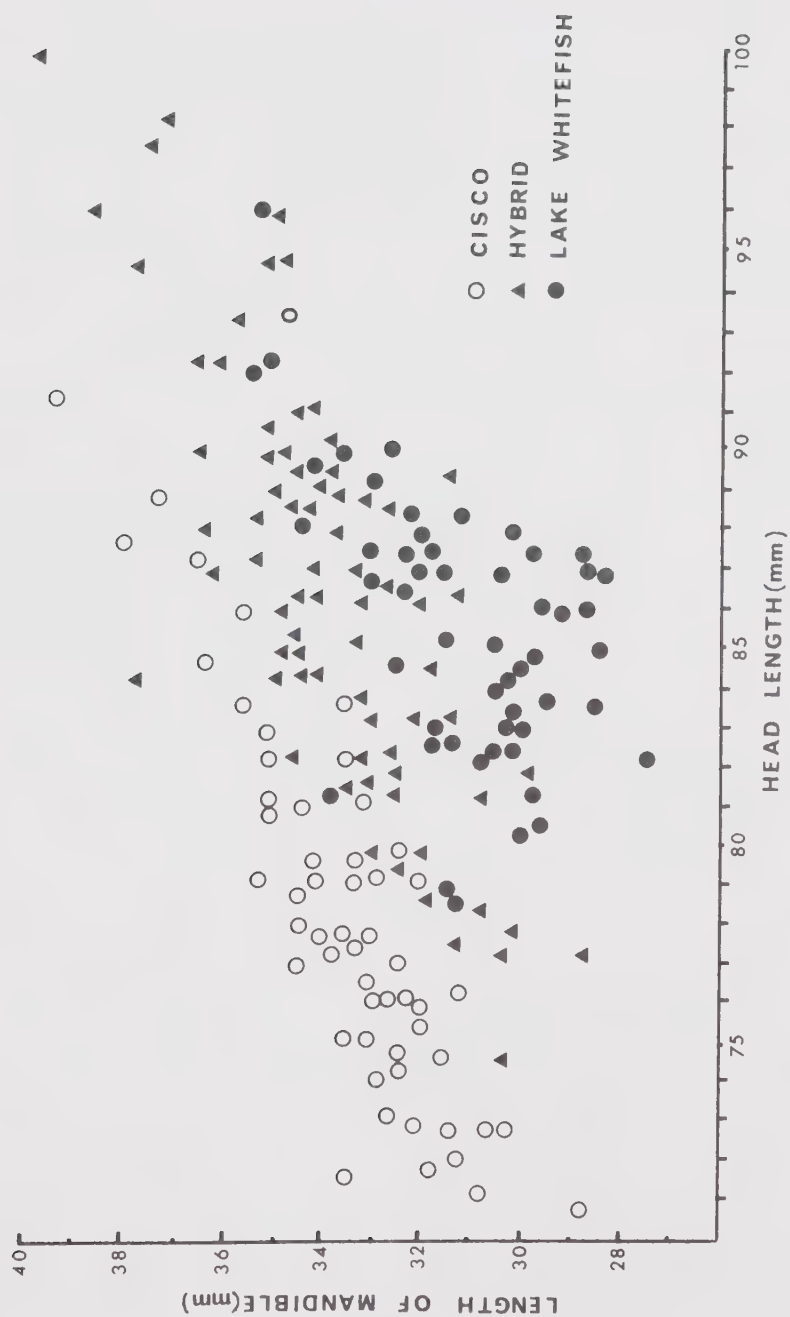


FIGURE 34. Relationship between length of base of adipose fin and standard length in lake whitefish, cisco and hybrids from Utikuma Lake.

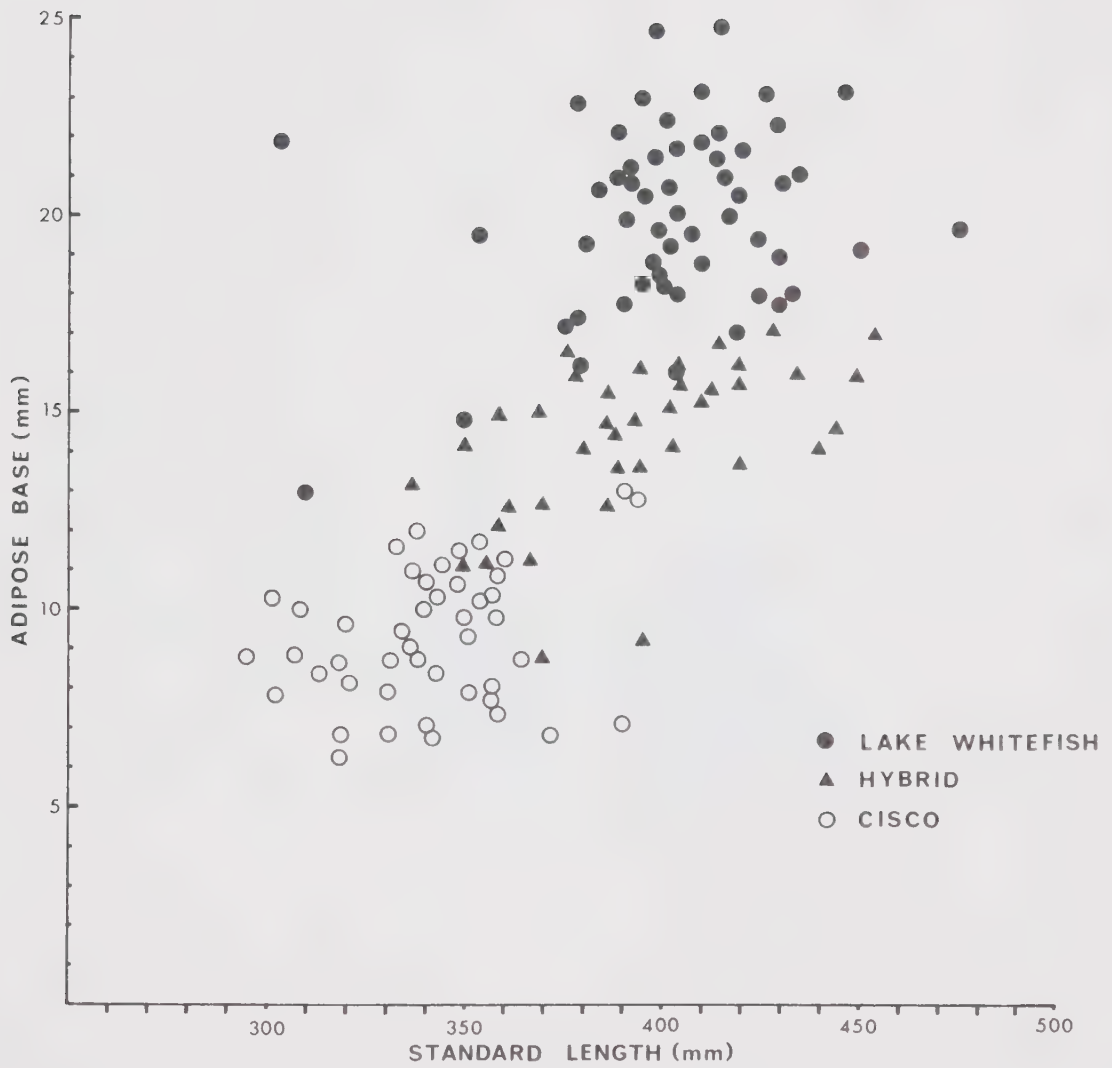


FIGURE 35. Character index for adult lake whitefish, cisco and hybrids from Utikuma Lake, calculated on gill raker number, premaxillary angle, ratio of standard length to adipose fin base and ratio of head length to mandible length.

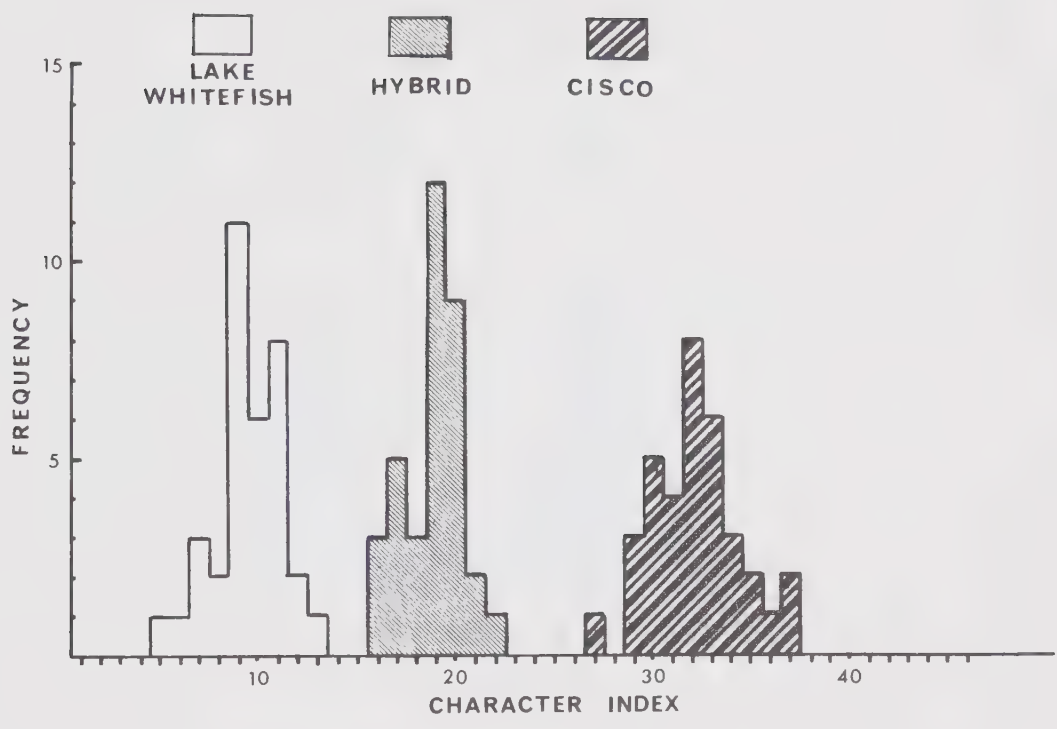


FIGURE 36. Character index for adult lake whitefish, cisco and hybrids from Nipisi Lake, calculated on gill raker number, premaxillary angle, ratio of standard length to adipose fin base and ratio of head length to mandible length.

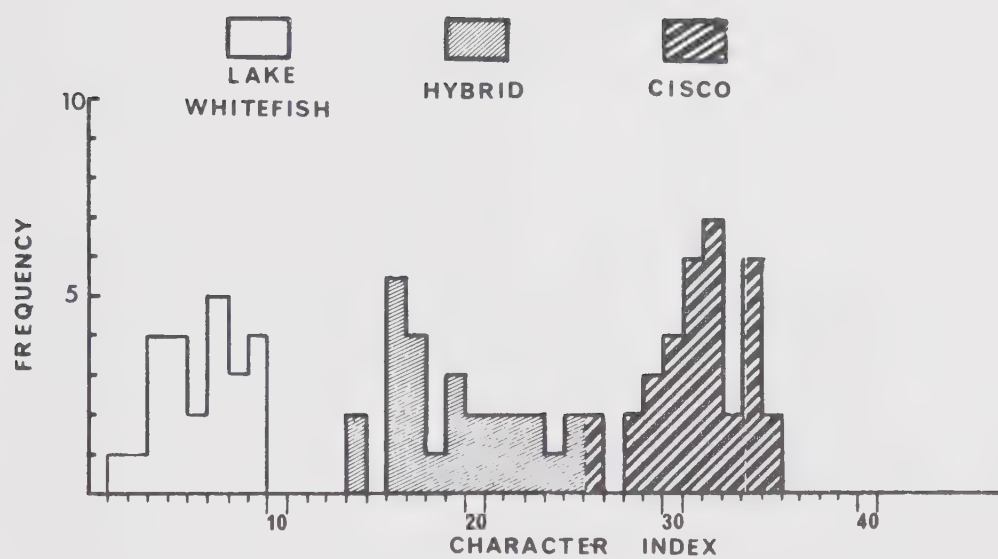
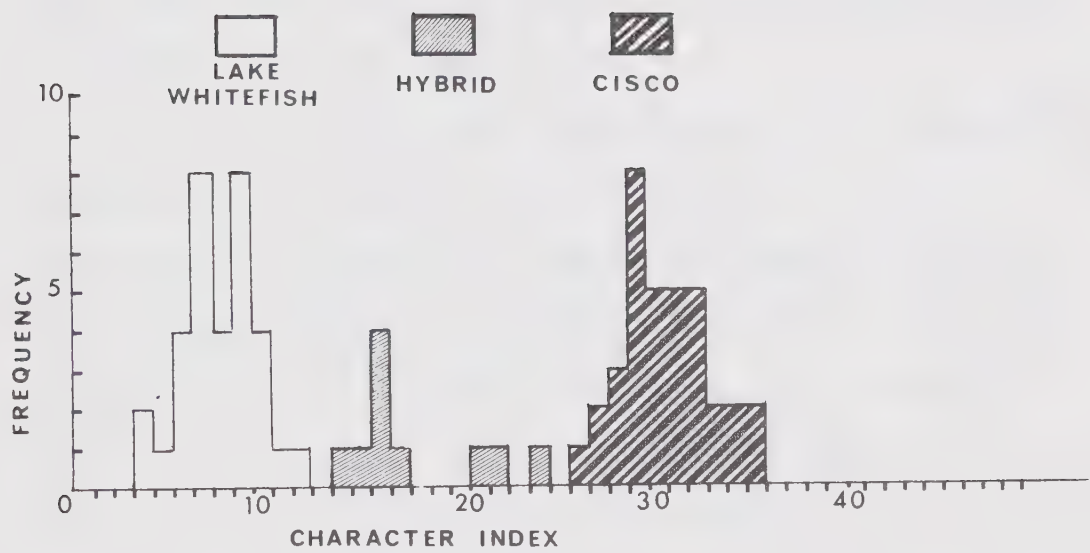


FIGURE 37. Character index for adult lake whitefish, cisco and hybrids from Wolf Lake, calculated on gill raker number, premaxillary angle, ratio of standard length to adipose base, and ratio of head length to mandible length.



from the parent species. Complete separation of hybrids and parents was not, however, demonstrated in Nipisi Lake. The character index of a very few individual hybrids and ciscoes was found to overlap. Considering the separation obtained between parent species and hybrids in fish from Utikuma and Wolf Lakes but having not obtained discrete separation between hybrids and ciscoes in Nipisi Lake one may infer that backcrossing between hybrids and ciscoes could be taking place in the latter lake.

In order to further identify hybrids on morphological grounds the combination of the three characters previously employed, but excluding gill rakers, was plotted against gill raker number. Results are shown in Figure 38 for Utikuma Lake samples, Figure 39 for Nipisi Lake samples and in Figure 40 for Wolf Lake samples. Complete separation between hybrids and parent species is obtained by this method. It is also noted that the two individuals from Nipisi Lake with gill raker counts of 44, fall into the hybrid grouping. This strengthens the evidence obtained in the plot of premaxillary angle against gill raker number that these individuals are in fact hybrids. The proximity of such individuals in both character index value and gill raker number to the cisco group may still be suggestive of backcrossing. Further support of this hypothesis is presented in the section on electrophoretic analysis.

FIGURE 38. Character analysis used to identify adult lake whitefish, cisco and hybrids from Utikuma Lake. (Character index calculated on premaxillary angle, ratio of standard length to adipose fin base and ratio of head length to mandible length.

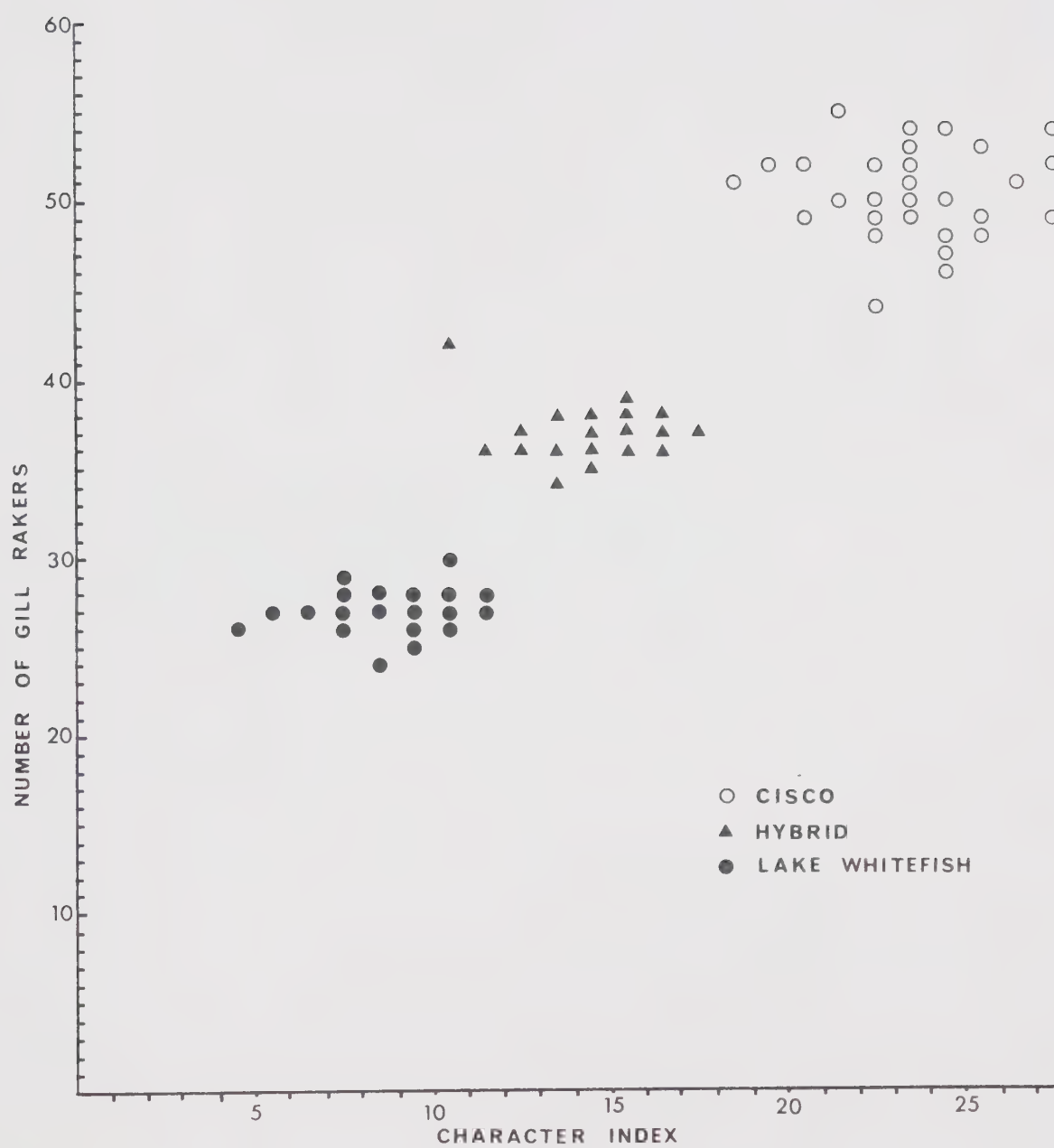


FIGURE 39. Character analysis used to identify adult lake whitefish, cisco and hybrids from Nipisi Lake. (Character index calculated on premaxillary angle, ratio of standard length to adipose fin base and ratio of head length to mandible length.

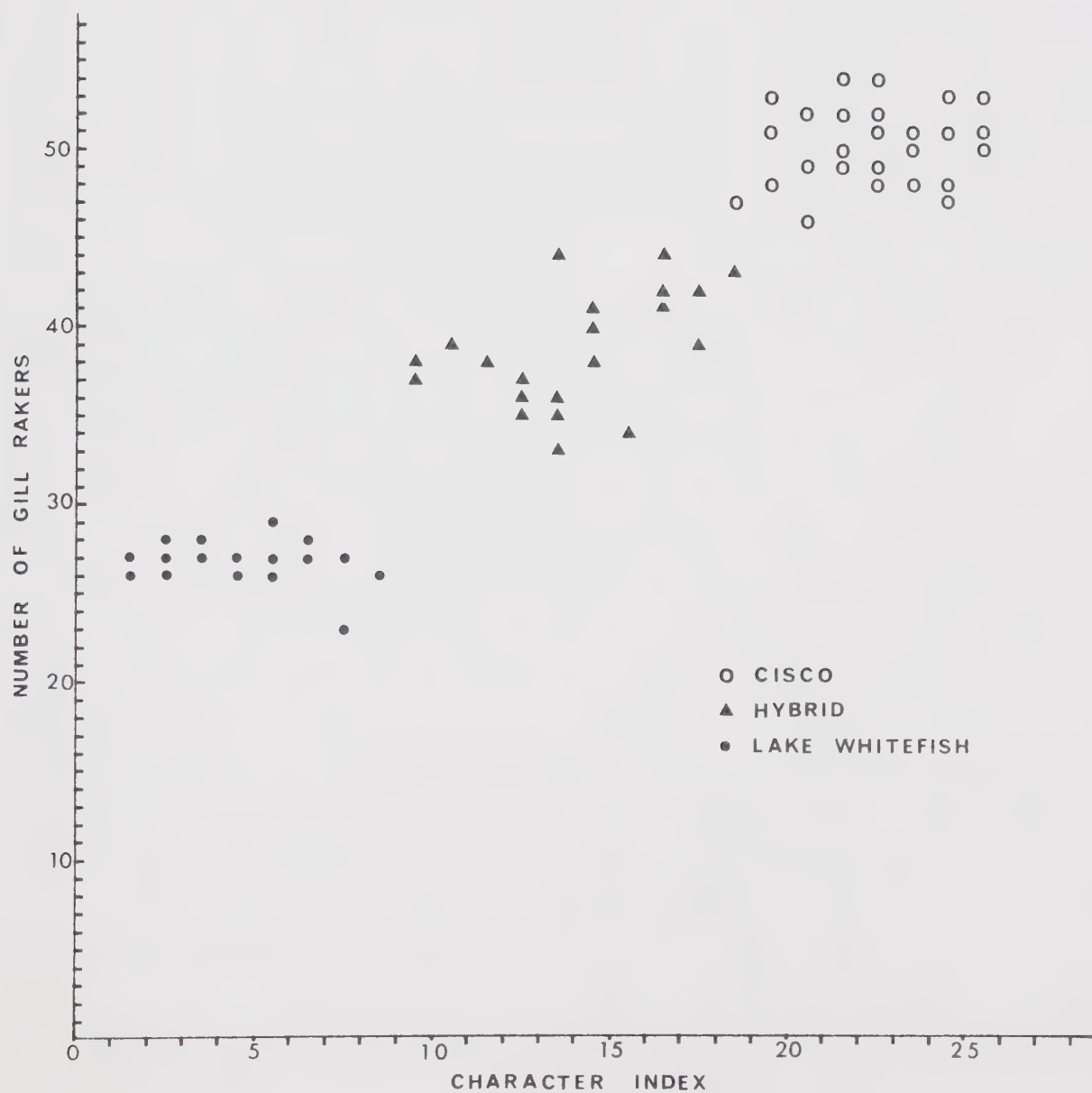
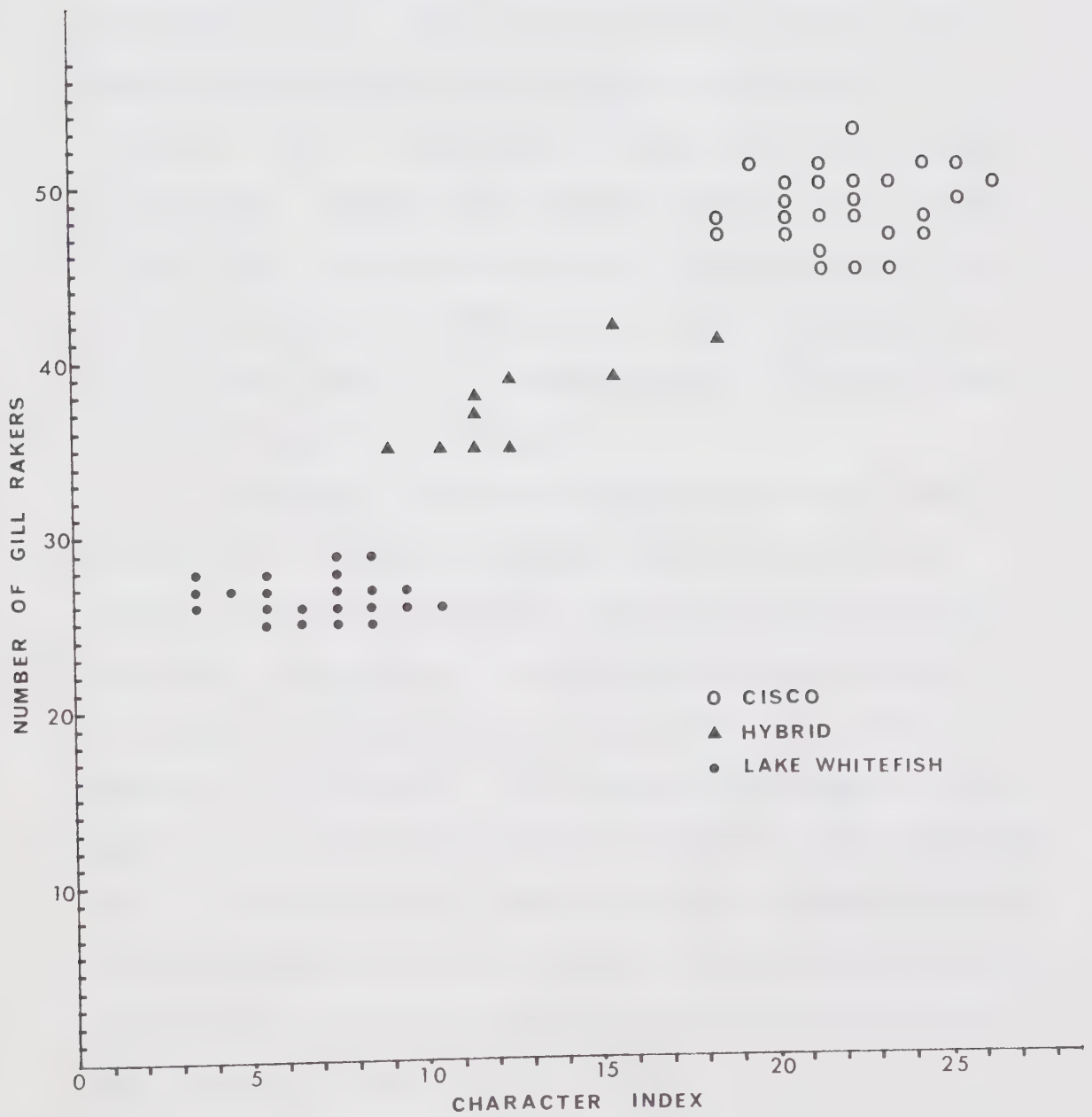


FIGURE 40. Character analysis used to identify adult lake whitefish, cisco, and hybrids from Wolf Lake. (Character index calculated on premaxillary angle, ratio of standard length to adipose fin base and ratio of head length to mandible length.)



B. Morphological Analysis of Juveniles from Artificial Crosses Using Utikuma Lake Parents

1. Gill Rakers. The sample of pure *C. clupearformis* was obtained from pooling the progeny of three lots. Each lot was the result of using one male and one female parent. The male parents had gill raker counts of 29, 27, and 26 and the female parents had counts of 26, 24 and 26 respectively. The sample of pure *C. artedii* was also obtained from the pooling of three lots. However, two of the lots were the result of using one female and two males while the third lot was obtained from a single male and a single female parent. The five male parents had gill raker counts of 46, 54, 50, 50 and 53. The three female parents had counts of 50, 54 and 50.

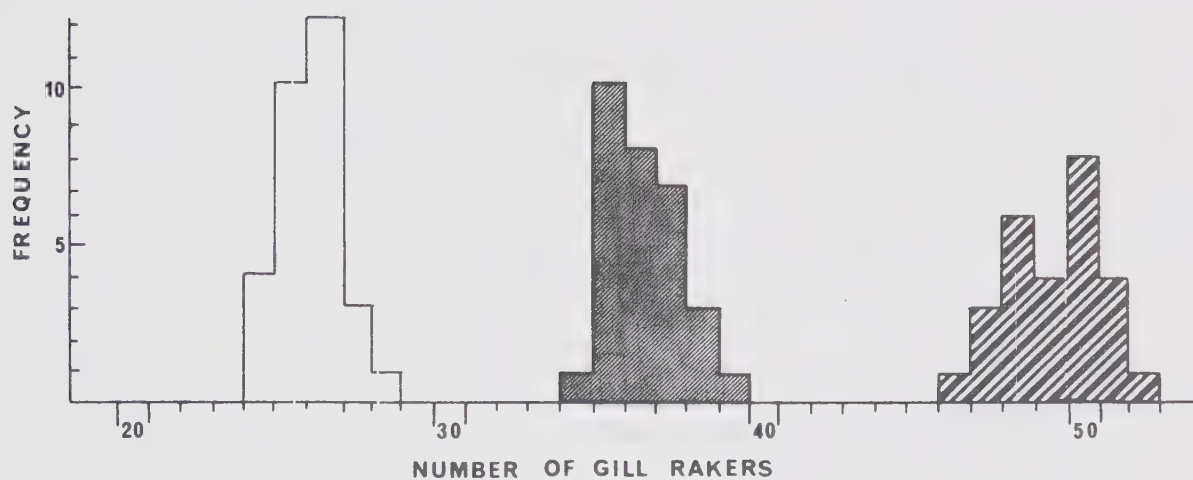
The sample of the first heterospecific cross (female whitefish X male cisco) was obtained from three pooled lots. Each lot represented the progeny of one female whitefish parent and one male cisco parent. The three female parents had gill raker counts of 26, 30 and 27, while the three male parents had counts of 52, 48 and 49. The reciprocal heterospecific cross (female cisco X male whitefish) was also obtained from three pooled lots. In producing each of these three lots one female cisco and two male whitefish were used as parents. The six male parents had gill raker counts of 27, 27, 28, 28, 27 and 25, while the three female parents had counts of 49, 47 and 52.

The first backcross sample was obtained by using a single hybrid male and three cisco females. The male parent had a gill raker count of 38 and the female parents had counts of 48, 49 and 52. The second backcross sample was obtained using the same hybrid male and three whitefish females with counts of 28, 28 and 26.

Gill raker counts of homospecific crosses, heterospecific crosses and presumed male hybrid backcrossed to *C. clupeaformis* and *C. artedii* females are shown in Figures 41 and 42. Complete separation between parent species and between parent species and F_1 's of reciprocal crosses is shown. In gill raker number it appears that the male parent in a heterospecific cross exerts dominance. A presumed male hybrid backcrossed to the parent species produced progeny with modal gill raker distribution between the F_1 's and the pure strains. It is noted that the range of gill raker number in backcrosses is greater than that observed in either one of the heterospecific crosses. This is in agreement with the findings of Svardson (1965). It is also noted that the progeny of the two separate backcrosses have gill raker counts which overlap with each other and slightly overlap with the highest counts of pure whitefish. Although there was no actual overlap with the progeny of the pure cisco cross, the highest gill raker count of the female cisco x male hybrid was only one less than the lowest count of the ciscoes. The ranges

FIGURE 41. Gill raker distribution of progeny of homospecific crosses and one heterospecific cross involving lake whitefish (W) and cisco (C) from Utikuma Lake.

FIGURE 42. Gill raker distribution of progeny of homospecific crosses, reciprocal cross and backcrosses involving lake whitefish, cisco and male hybrid (H) from Utikuma Lake.



♀W x ♂W

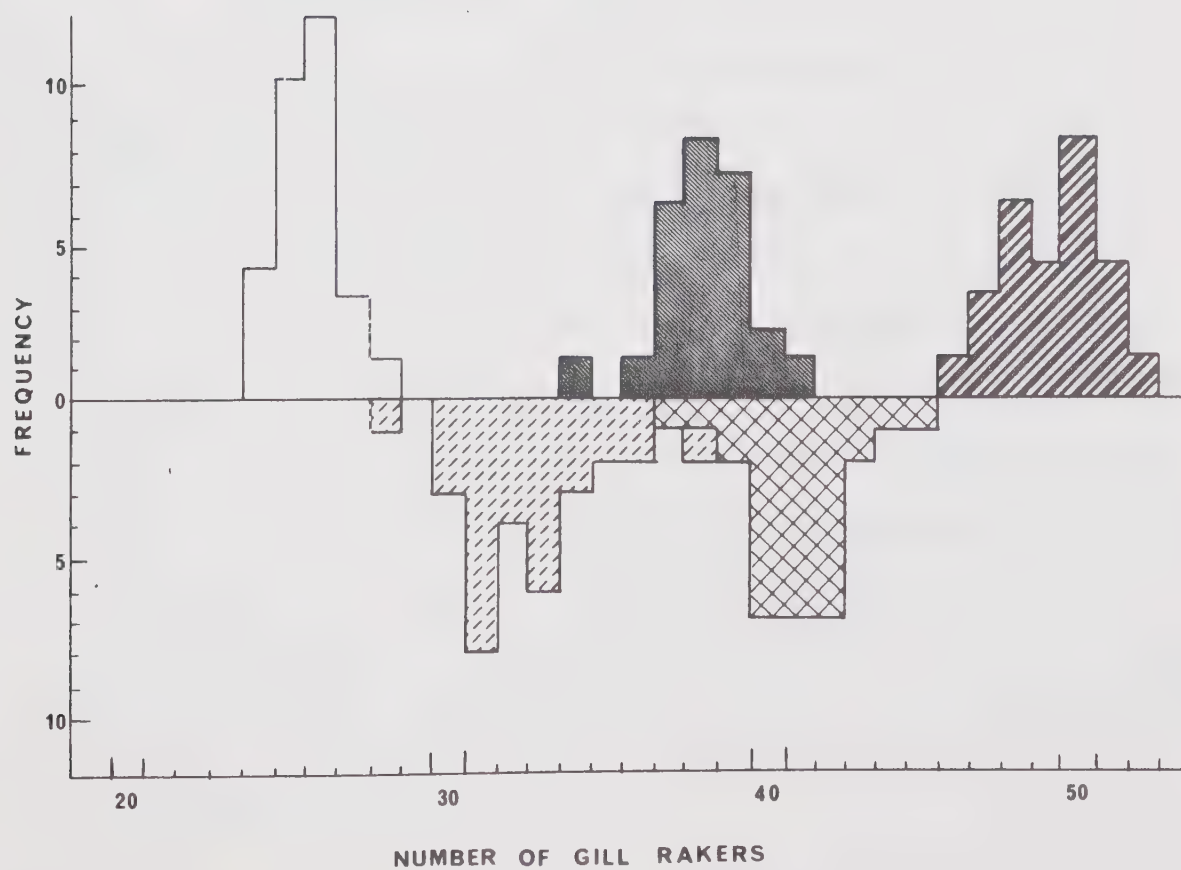
♀W x ♂C

♀C x ♂C

♀C x ♂W

♀W x ♂H

♀C x ♂H



and means of gill raker counts of selected wild samples from Utikuma Lake and of artificial crosses using Utikuma Lake parents are summarized in Table 2.

2. Premaxillary Angle. Some difficulty was encountered in measuring the premaxillary angle of juvenile fish mainly because of the soft nature of the mouth parts when the specimens were in fresh condition. This was overcome by measuring the character after the specimens had been hardened in formalin and by reading the angle with the aid of magnification. The results along with measurements on Utikuma Lake wild stocks are summarized in Table 3.

From Table 3 it is clear that the juvenile whitefish and ciscoes produced by artificial crossing have considerably lower mean premaxillary values than wild adults. The combined reciprocal crosses (F_1 's) also have a lower mean value than that of presumed adult hybrids. Further, there is no overlap between the pure whitefish juveniles and artificially produced F_1 hybrids as there is in between wild adult whitefish and wild hybrids. From this it would appear that the final angle of the premaxillary has not been determined at the size at which measurements were made on the juveniles. However, since the three groups have actually better separation in this character than do adult fish, the character is useful in discriminating between F_1 hybrid juveniles and juveniles of the parent species.

TABLE 2. Ranges and means of first arch gill raker counts of selected samples of coregonines from Utikuma Lake and of progeny of artificial breeding experiments using parents from Utikuma Lake. (Size of sample indicated by numbers in parentheses.)

	WILD ADULTS		ARTIFICIAL CROSSES	
	RANGE	MEAN	RANGE	MEAN
<i>C. clupearformis</i>	25-30	27.1 (50)	24-28	25.6 (30)
Hybrids	33-42	36.9 (75)	34-41	37.1 (56)*
<i>C. artedii</i>	44-55	50.0 (103)	46-52	49.1 (27)
♀ W X ♂ H	-	-	28-38	32.5 (30)
♀ C X ♂ H	-	-	35-45	40.8 (30)

*All F₁'s combined.

TABLE 3. Premaxillary angle of progeny of artificial crosses (using Utikuma Lake parents) and wild adult coregonines from Utikuma Lake (Size of sample indicated by numbers in parentheses.)

	WILD ADULTS		ARTIFICIAL CROSSES	
	RANGE	MEAN	RANGE	MEAN
<i>C. clupeaformis</i>	84-117	100.1 (62)	89-101	95.1 (30)
Hybrids	74-98	84.3 (38)	61-88	71.7 (60)
<i>C. artedii</i>	33-65	46.5 (80)	30-47	39.3 (27)
♀ W X ♂ H	-	-	62-87	80.3 (30)
♀ C X ♂ H	-	-	53-66	60.1 (30)

A character index using the same four characters as used for adults was calculated for each individual juvenile. Since juveniles of all groups of artificial crosses were of relatively the same size and since there was considerable overlap in head length between individuals of the various groups, the problem of allometric growth in the ratios: standard length to adipose base, and head length to length of mandible, would not be a significant source of error. The use of the latter ratios in constructing a character index was, therefore, considered valid.

A graph combining the four characters for each individual of the six artificially produced groups (W X W, C X C, C♀ X W♂, C♂ X W♀, C♀ X H♂ and W♀ X H♂) is shown in Figure 43. The method permits discrimination between juveniles of parent species as well as between juveniles of heterospecific crosses (all F₁'s combined) and parent species. Backcrosses overlap with F₁'s as well as with pure strain whitefish.

The index value of three of the four characters (excluding gill rakers) was plotted against gill raker number. Figure 44 gives the results using parental strain juveniles and combined heterospecific crosses. Figure 45 shows the plot of parental strain in relation to the two backcrosses. A distinct separation is again achieved between parental strains and combined F₁'s. Known hybrids are, therefore, morphologically intermediate in relation to the parental species in the characters used.

FIGURE 43. Character index for juvenile lake whitefish, cisco, reciprocal crosses and two backcrosses (Samples from artificial breeding experiments. Character index calculated from same characters as used for adults.)

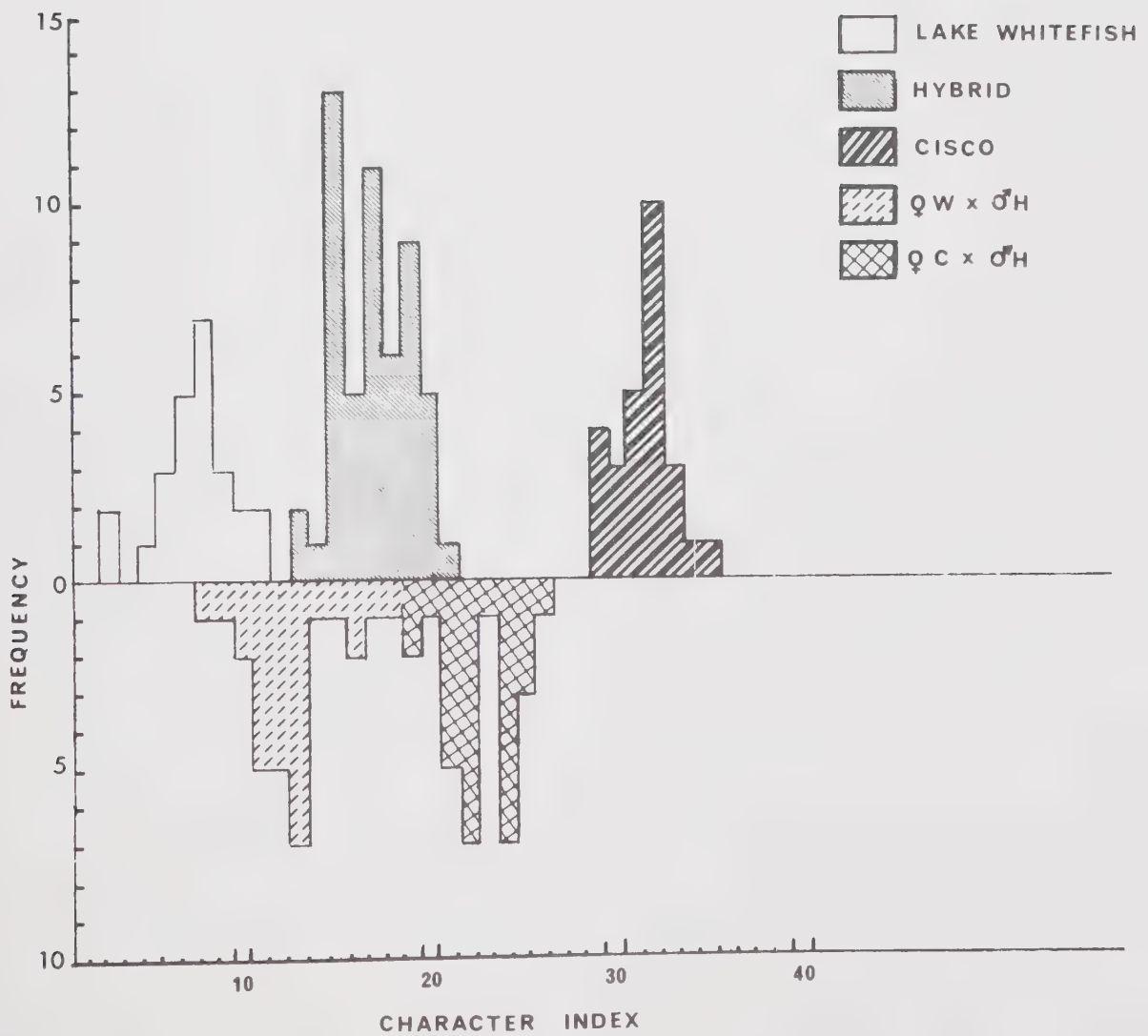


FIGURE 44. Character analysis used to identify juvenile lake whitefish, cisco and combined reciprocal crosses (Samples from artificial breeding experiments.) Character index calculated from same characters as used for adults.

FIGURE 45. Character analysis used to identify juvenile lake whitefish, cisco, and two backcrosses (samples from artificial breeding experiments). Character index calculated as above.

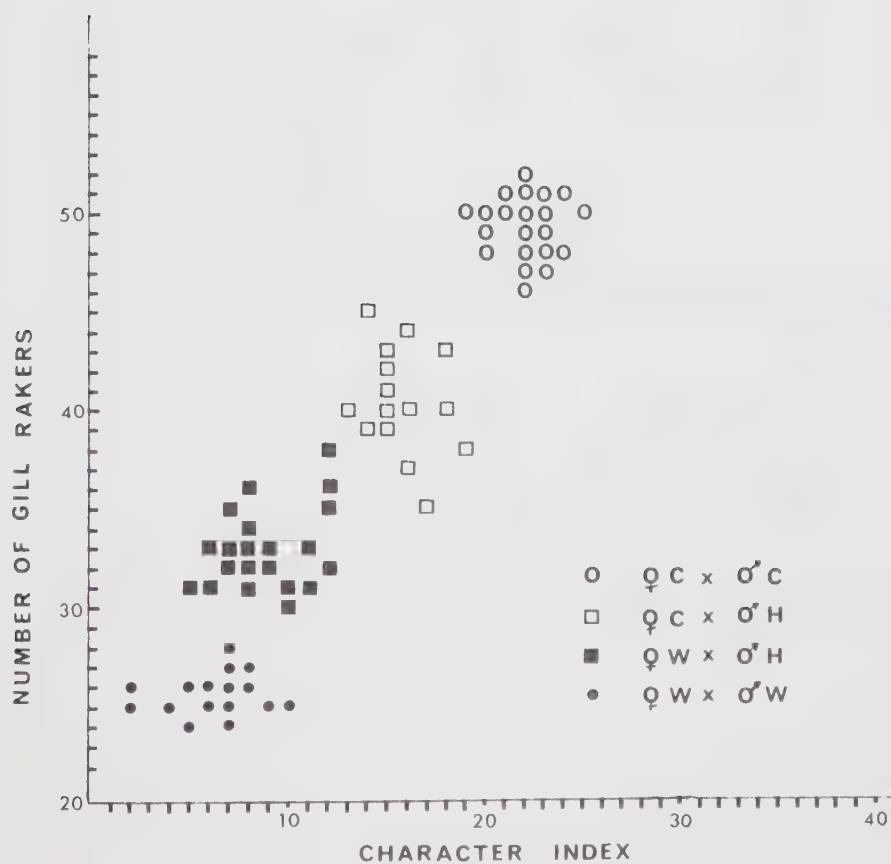
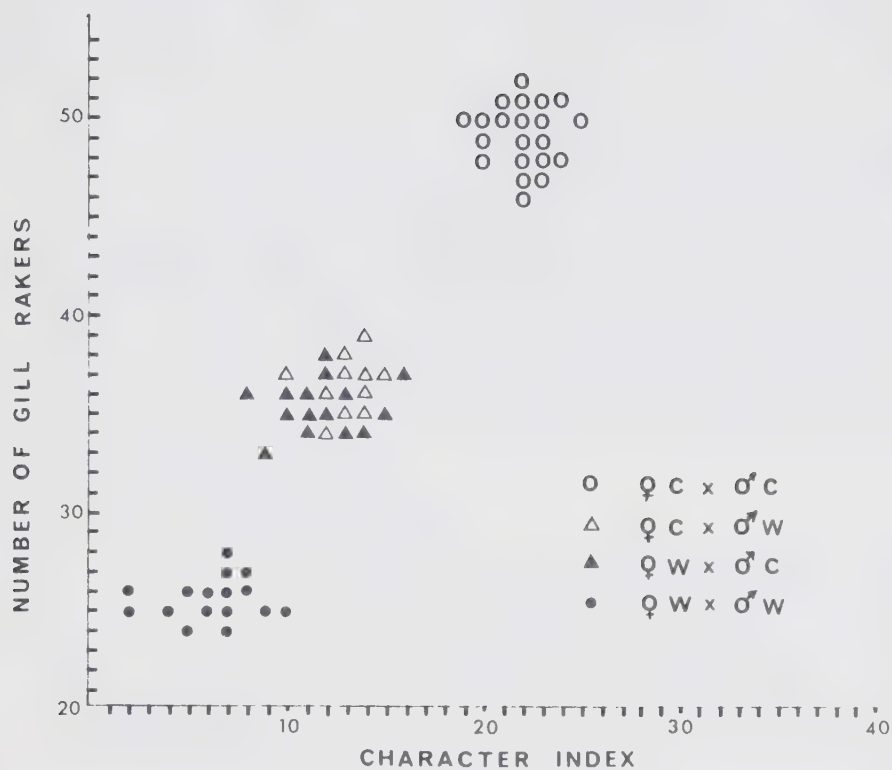


Figure 45 shows that it is possible to distinguish the backcrosses from the juvenile parental species by this type of plot. However, a comparison of Figures 44 and 45 shows that it would not be possible to distinguish many backcrosses from F_1 's.

C. Egg Morphology

By the method described (see material and methods) for determining the difference in the diameter of eggs of *C. clupeaformis*, *C. artedii* and presumed hybrids, it was found that the average egg diameters were 2.78 mm., 1.99 mm. and 2.17 mm. respectively. It is apparent, therefore, that the egg size of hybrids is intermediate between that of whitefish and ciscoes. This may be taken as evidence of the intermediacy of hybrids in an additional character.

D. Electrophoretic Analysis

Electrophoretic analysis of muscle proteins was carried out as follows:

- (1) on wild parental species and presumed hybrids in lakes where all three groups existed; except North Buck Lake;
- (2) on parental species in sympatry where no hybrids were found;

- (3) on allopatric specimens of *C. clupeaformis* and *C. artedii*, and
- (4) on samples of all artificial crosses and their parents.

The two species can be identified by the first distinct protein bands nearest the origin. All *C. artedii*, irrespective of lake or origin, have a "slow" band which is designated as #1. All *C. clupeaformis* lack band #1 but have a band which has migrated further in the gel which may be termed a "fast" band and is designated as band #2. Presumed hybrids exhibit both band #1 and band #2. Figure 46 is a diagrammatic representation of the muscle protein patterns. The protein patterns of artificially reared *C. clupeaformis*, *C. artedii* and F₁ hybrids were identical to those of the respective wild parents and the presumed wild hybrids. The backcrosses yielded approximately a 50:50 ratio of hybrid type to the parental type with which the hybrid was crossed.

Figure 47 shows the pattern obtained from fifteen fish from Utikuma Lake. (The type of fish is identified at the origin of each sample). Figure 48 depicts twelve specimens from Nipisi Lake while Figures 49 and 50 show allopatric specimens of whitefish and cisco from Smoke Lake and Square Lake respectively. Figure 51 shows the protein pattern of parents from Utikuma Lake used in artificial crosses and Figure 52 shows the offspring of homospecific

FIGURE 46. Diagrammatic representation of muscle protein banding of cisco (C), lake whitefish (W) and hybrid (H).

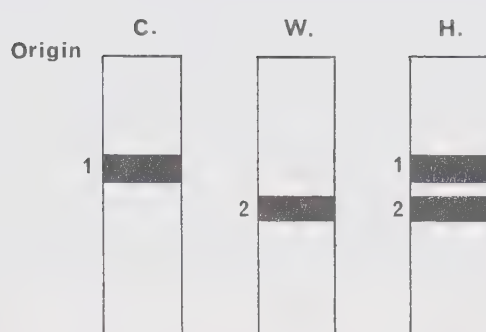


FIGURE 47. Muscle myogen electropherograms of lake whitefish (W), cisco (C) and hybrid adults (H) from Utikuma Lake.

FIGURE 48. Muscle myogen electropherograms of lake whitefish (W), cisco (C) and hybrid adults (H) from Nipisi Lake.

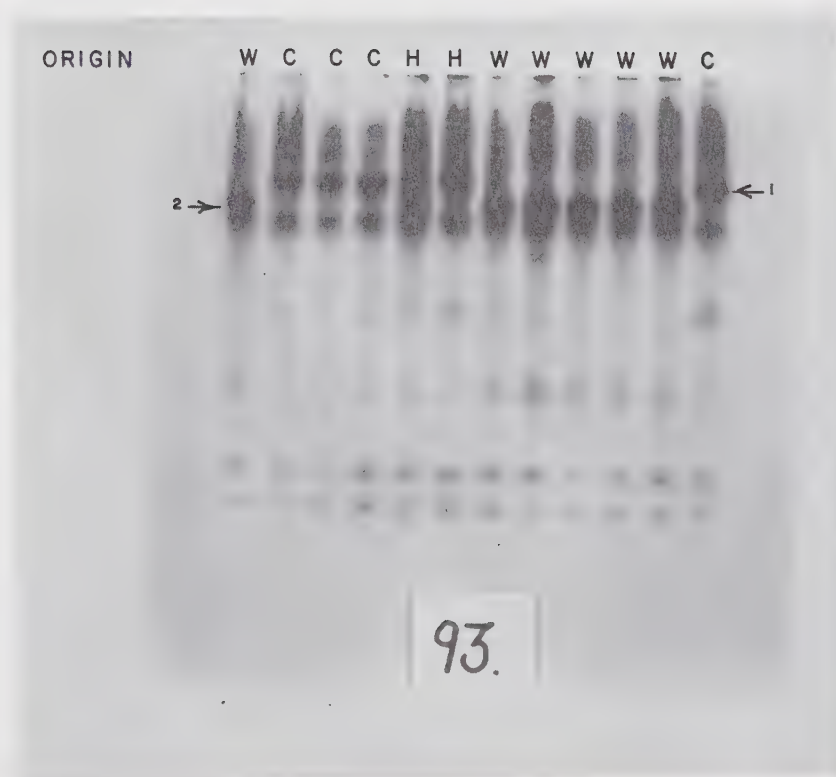
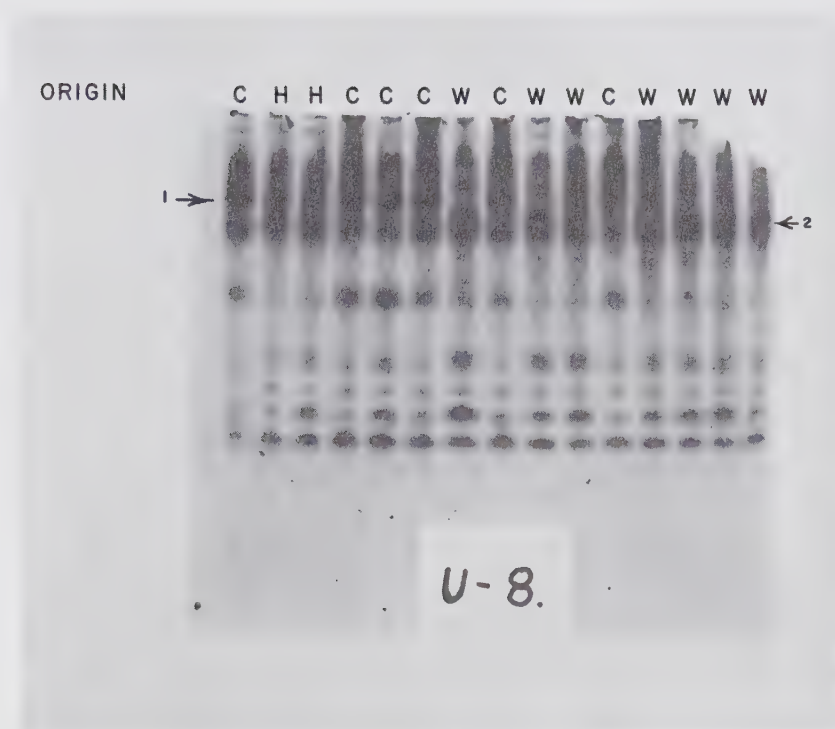


FIGURE 49. Muscle myogen electropherograms of lake whitefish adults from Smoke Lake.

FIGURE 50. Muscle myogen electropherograms of cisco from Square Lake.

ORIGIN

W W W W W W W W W W W W W

← 2

19.

ORIGIN

C C C C C C C C C C C C C C C

← 1

22.

FIGURE 51. Muscle myogen electropherograms of lake whitefish (W) and cisco (C) parents from Utikuma Lake, used in artificial breeding experiments.

FIGURE 52. Muscle myogen electropherograms of progeny of homospecific crosses and one heterospecific cross. Cisco (C), lake whitefish (W).

ORIGIN

C W W W W W W W W C W W

1 →

← 2

103.

ORIGIN

C C W W W W W W W C C C C C
X X X X X X X X X X X X X X
C C W W W W W W W W W W W W

→ 1
→ 2

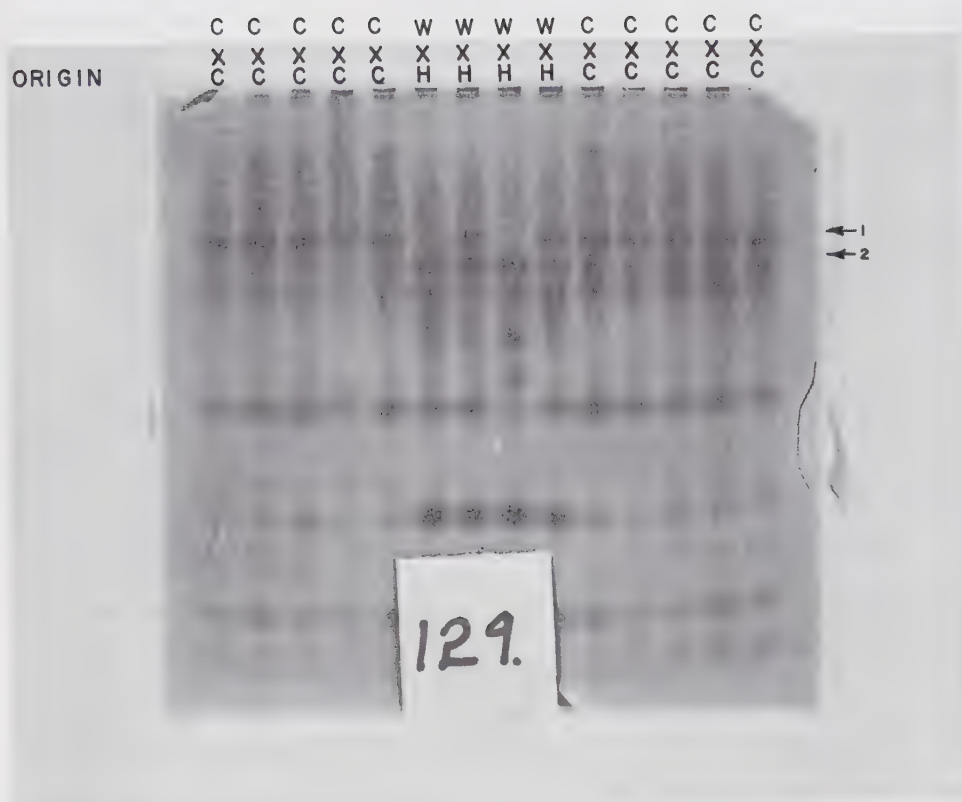
132.

crosses and a heterospecific cross. Figure 53 depicts progeny of the female whitefish X male hybrid backcross, along with individuals of a homospecific cross.

Since no specimens showing both bands of #1 and #2 were obtained from allopatric populations and since the presumed wild hybrids showed a protein pattern identical to that of the F_1 progeny obtained from artificial crosses, it is concluded that the presumed wild hybrids are in fact hybrids although not necessarily all F_1 types. In this regard it is of interest to refer back to the two specimens from Nipisi Lake which had gill raker counts of 44. According to the plot of premaxillary angle against gill raker number, and also by the character index method of identification these specimens appeared to be hybrids. In protein pattern however one of these fish showed the hybrid pattern while the other had a cisco pattern. It is suspected therefore that the one showing the cisco-like protein pattern is a backcross, i.e. hybrid x cisco parent. The other specimen could either be a backcross or an F_1 hybrid.

The protein pattern obtained on all other specimens, on which electrophoresis was carried out, confirmed the original identification of the specimen. However, this is not to say that all specimens were correctly identified owing to the possibility of backcrossing being involved.

FIGURE 53. Muscle myogen electropherograms of progeny of a backcross and cisco x cisco. Hybrid (H) ♂ x lake whitefish (W) ♀, and a homospecific cross, cisco x cisco (C).

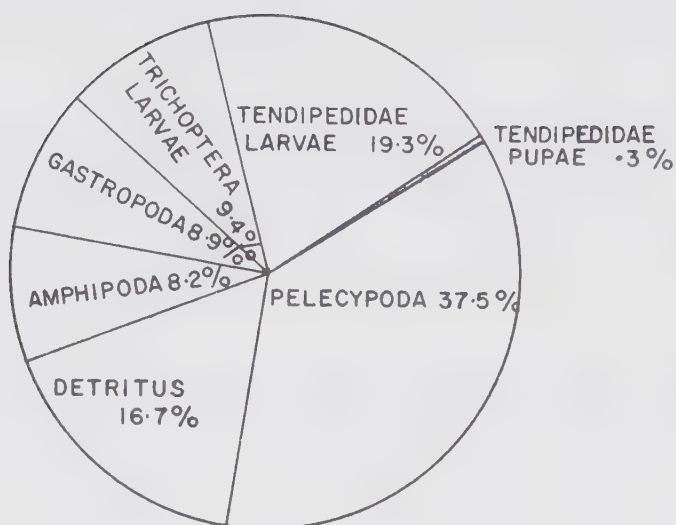


E. Food Habit Studies

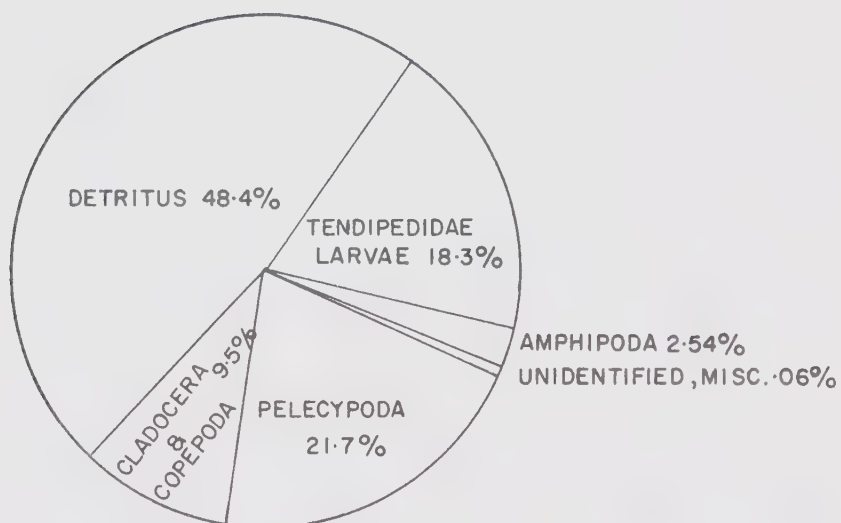
The stomachs of 30 lake whitefish, 30 ciscoes and 12 hybrids taken in Utikuma Lake in May and June, 1971, were analyzed as to food content. In both lake whitefish and ciscoes 13 per cent of the stomachs were empty. None of the hybrid stomachs was empty. In determining the per cent contribution of food items to the May-June diet of the three groups of fish, only the stomachs which contained food were used. The results of this analysis is shown in Figure 54. Several differences in what may be considered as the spring diet of lake whitefish, hybrids and ciscoes in Utikuma Lake, are observable. Detritus, which consists of organic debris such as pieces of plant stems, bark, etc., sand grains, fragments of shells and invertebrate exoskeleton, makes up a considerably larger percentage of the volume of stomach content of hybrids than that of whitefish and cisco. This may suggest that hybrids are not as efficient in their selection of food items as the parent species. The remainder of the hybrid diet resembles that of the bottom feeding lake whitefish, more than that of the plankton feeding cisco. The relatively large contribution by Pelecypoda and Tenedipodidae larvae are indicative of this. There is also evidence however that hybrids have more of a tendency to utilize plankton than lake whitefish as shown by the fact that almost 10 per cent of the stomach content

FIGURE 54. Graphical comparison of percentage of volume of stomach contents contributed by different food items in lake whitefish, hybrids and cisco from Utikuma Lake.

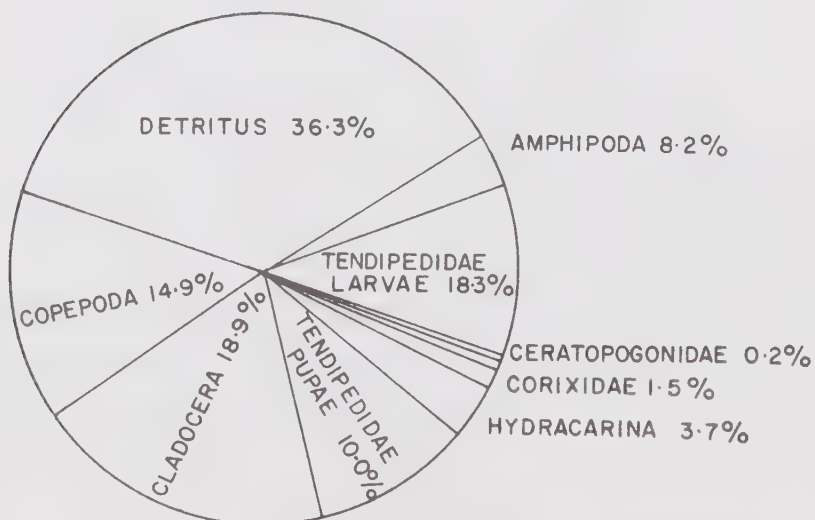
LAKE WHITEFISH



HYBRID



CISCO



volume was made up of cladocerans and copepods while these items did not contribute to the diet of lake whitefish.

F. Age - Growth Studies

Samples of coregonines used in age and growth studies were obtained from Wolf Lake in the latter part of October and during November and December; from Utikuma Lake in November and January, and from North Buck Lake in October and early April. Although the samples were not all taken during the same time period, they were taken during the season of little or no growth and should be comparable. Comparison of the mean standard length of lake whitefish, hybrids and ciscoes at various ages is shown in Table 4 for North Buck Lake, in Table 5 for Utikuma Lake, and in Table 6 for Wolf Lake.

While statistical comparisons of the means was not made due to lack of sufficient numbers of fish in some age classes and the wide variation in sample size, the data are relatively consistent for the three lakes in indicating that the rate of growth of lake whitefish exceeds that of hybrids and that of hybrids exceeds that of ciscoes. The rate of growth of hybrids is, therefore, generally intermediate with the exception of age classes VI and VII from Utikuma Lake in which cases the hybrids are slightly larger than lake whitefish of the same age. No explanation for this exception seems apparent.

TABLE 4. Comparison of the mean standard lengths (mm.) of three age classes of lake whitefish, hybrids, and ciscoes from North Buck Lake. Sample size in parentheses.

TYPE	NUMBER OF ANNULI		
	III	IV	V
Lake Whitefish	339.5 (6)	375.4 (19)	390.0 (26)
Hybrid	322.7 (3)	360.8 (12)	384.6 (17)
Cisco	304.0 (3)	334.5 (24)	358.0 (6)

TABLE 5. Comparison of the mean standard lengths (mm.) of four age classes of lake whitefish, hybrids and ciscoes from Utikuma Lake. Sample size in parentheses.

TYPE	NUMBER OF ANNULI			
	IV	V	VI	VII
Lake whitefish	376.8 (7)	396.7 (18)	406.6 (24)	391.3 (4)
Hybrid	370.2 (9)	387.3 (27)	407.2 (28)	400.4 (7)
Cisco	328.9 (14)	342.5 (34)	347.9 (17)	487.5 (3)

TABLE 6. Comparison of the mean standard lengths (mm.) of five age classes of lake whitefish, hybrids and ciscoes from Wolf Lake. Age class VII omitted due to absence of hybrids. Sample size in parentheses.

TYPE	NUMBER OF ANNULI				
	III	IV	V	VI	VIII
Lake whitefish	337.1 (10)	366.5 (47)	392.1 (37)	407.6 (12)	438.3 (3)
Hybrid	288.8 (4)	305.0 (5)	323.8 (4)	331.7 (3)	373.6 (5)
Cisco	239.1 (7)	256.8 (54)	262.6 (49)	271.2 (25)	283.1 (10)

Several investigators of hybridization have referred to the superior growth or heterosis effect. Hubbs and Hubbs (1933) demonstrated the phenomenon of heterosis in hybrid sunfish (Centrarchidae). Svardson (1965) showed that the growth of F₁ hybrids of *C. pidschian* X *C. oxyrinchus* was 4.8 per cent greater than that of the parent species. Gasowska (1958) in referring to hybrids of *C. l. maraenoides* X *C. albula* L., states that heterosis of growth affects the hybrids originating from the small whitefish (cisco) female. Preliminary evidence obtained in this study does not support the heterosis phenomenon.

ISOLATING MECHANISMS

A. Temporal Isolation

Investigations were made to explore the differences in spawning time of the parental species in sympatry, to determine whether this factor played a part in preventing or reducing the chances of hybridization.

Adult whitefishes spawn generally from the late fall period in open water through early winter under ice cover. Bidgood (pers. comm.) found ripe *C. clupeaformis* individuals in Pigeon Lake from the latter part of September (water temperature 9° C) to the latter part of January (temperature 1° C). Pritchard (1930), in his work on spawning habits of *C. artedii*, indicates that this

species begins to spawn at about the second week in November and continues for three weeks or longer in water temperatures dropping from 6.1° to 3.3° C. He further suggests that ciscoes commence spawning about two weeks later than lake whitefish. Colby and Brooke (1970) cite work that indicates that fall temperatures must drop early to 6.1° C and the decrease to optimum temperatures for development must be steady (these criteria being in part, necessary for strong year classes of lake whitefish).

Intensive investigations to document the entire spawning period of sympatric whitefishes were not undertaken in the present study, however, sufficient observations were made in several of the lakes to provide information on temporal isolation.

Wolf Lake

The first ripe individuals of both species were taken on October 5, 1968, in water temperatures of 9.6° C. At this date both species were still scattered and no obvious concentrations of spawners were encountered on known spawning grounds. On October 11 (water temperatures 8.2° C) in a sample of 27 lake whitefish and 20 cisco, all males extruded milt when

slight pressure was applied to the abdomen and 80 per cent of the females of both species released eggs when moderate pressure was applied. These fish were apparently the early spawners of both species; the condition of the next catches on October 25 and 26 was noticeably different. On these dates the water temperature had dropped to 6.6° C and 4.2° C on two separate spawning areas in the lake. Out of 63 female and 52 male ciscoes, 27 per cent of the former and 73 per cent of the latter were ripe. Ten per cent of the females were spent and the remainder were not quite ready to spawn. Of 14 whitefish taken at the same time, 83 per cent of the females were ripe and the remainder were spent. All male whitefish were in ripe or partially spent condition. On December 1, all female whitefish examined were spent but some milt could still be extruded from a small number of males. Eggs were still freely flowing from a considerable number of female ciscoes as they were taken from nets.

There is, therefore, almost a complete overlap of spawning time in both species in Wolf Lake except for the fact that the spawning period in ciscoes is somewhat more prolonged than it is in lake whitefish.

Utikuma Lake

Spawning in both species begins in the last week in October and reaches its peak about the end of the first week of November. The water temperature in 1969 dropped from 4.1°C to 2°C during this period. In 1971 the lake had completely frozen over by October 30 and spawning activity was very heavy in both lake whitefish and ciscoes between that date and November 5. In 1970 both species were very abundant in the Utikuma River during the first week of November and were actively spawning. Spawning was observed to begin at about 5:30 in the evening and continued until 6:30 the following morning. By November 14 of that year, the spawning of lake whitefish in the river had completely subsided. Small schools of ciscoes were still present although none of these fish was observed spawning.

The overlap in spawning time of the two species in Utikuma Lake appears to be even more pronounced than in Wolf Lake, with most of the activity confined to about a three week period. Temporal isolation appears to be practically nonexistent.

Touchwood Lake

The first spawning observations were made on Touchwood Lake on September 26, 1969, when it was observed that some male whitefish would release milt with moderate pressure being applied.

None of the females examined were in ripe condition. The next observations were made on October 24 (water temperature 6°C throughout). All male and female lake whitefish captured, were in ripe condition but both male and female ciscoes had not yet reached this condition. On October 31 (water temperature 4.5°C) the lake whitefish spawning activity appeared to be at, or just passing its peak. Difficulty was encountered, however, in finding a sufficient number of ripe male ciscoes to carry out artificial crossing. None of the female ciscoes were in ripe condition. In the period, November 4 to 8 most of the whitefish females had left the spawning grounds and out of eleven captured, 10 were completely spent and one partially spent. Males, however, were still fairly abundant and the majority of them were still releasing milt. At this time in a sample of 148 female ciscoes, 28 were ripe and the remainder were not yet in spawning condition. Males of this species were in ripe or near ripe condition.

Temporal isolation appears to be fairly well developed in Touchwood Lake but not sufficiently so to completely prevent hybridization.

Cold Lake

Samples of lake whitefish and ciscoes were taken on November 6, 13, 20 and 24, 1970, to investigate temporal isolation, with the following results.

On November 6, 80 per cent of a sample of 25 female whitefish were spent or partially spent. The remainder were ripe or approaching that condition. Male whitefish all appeared to be partially spent but most specimens still extruded milt with pressure on the abdomen. Ten per cent of the male ciscoes were ripe while milt could not be expressed from the remainder. Approximately 21 per cent of female ciscoes were ripe with the remainder not being ready to spawn.

On November 13, 93 per cent of female whitefish were spent, the remainder partially spent. All male whitefish were partially spent. Approximately one-third of the female ciscoes were spent or partially so while the remaining two-thirds were not yet ripe. About 50 per cent of male ciscoes were ripe.

On November 20 the samples indicated a condition in both lake whitefish and ciscoes which was very similar to that found a week earlier except that most male ciscoes now extruded milt freely.

On November 24 all female whitefish sampled were spent. Approximately 50 per cent of female ciscoes were ripe, a small percentage partly spent, and the remainder not yet ripe. About 80 per cent of male ciscoes were ripe. The remaining 20 per cent were not yet ready to spawn.

In addition to the above observations, it has been noted during the commercial fishery for ciscoes that the main spawning period appears to be during the first two weeks of December. Peak spawning periods for the two species, therefore, are approximately one month apart. However, as in Touchwood Lake there are some individuals of both species in spawning condition at the same time. There is sufficient temporal isolation in these two lakes to seriously reduce the opportunity for hybridization but it is insufficient to eliminate the opportunity entirely.

B. Habitat Isolation

In the Utikuma River, spawning areas consisted mostly of coarse sand and a small amount of gravel, in water depth of .5 to .75 meters. Both species were taken in ripe condition on these areas in evening seine hauls when spawning was actively in progress, so it can be assumed that both species were using this type of substrate.

In Wolf Lake the main spawning area was located in about 2 meters of water on a very flat, firm bottom. Ekman dredge samples of the surficial sediments indicated that the material was a mixture of sand and silt with the latter predominating. Late afternoon and evening net sets of one and two hour duration

during the spawning season caught ripe individuals of both sexes of both species.

The substrate of a major spawning ground in Cold Lake consists primarily of sand with some silt and occasional small stones, covered by 2 to 4 meters of water. Ripe lake whitefish were captured in the area in early November and ciscoes congregate on the area in very large numbers in early and mid-December. Both species, therefore, can be assumed to utilize at least this one area of the lake.

Habitat isolation does not appear to be a factor in the three lakes in which observations were made, hence, this would not be an important mechanism in reproductive segregation. Pritchard (1930) found eggs of lake whitefish and ciscoes in the same ground in the Bay of Quinte, Lake Ontario. Dryer and Beil (1964) state that *C. artedii* show no preference for a particular bottom type in Lake Superior. This would not seem to be so in Alberta unless ciscoes are utilizing the same area as lake whitefish purely by chance.

C. Ethological Isolation

Mayr (1963) points to ethological isolation as often being the most important single mechanism to prevent interbreeding. Because of the difficulty in making observations on actual

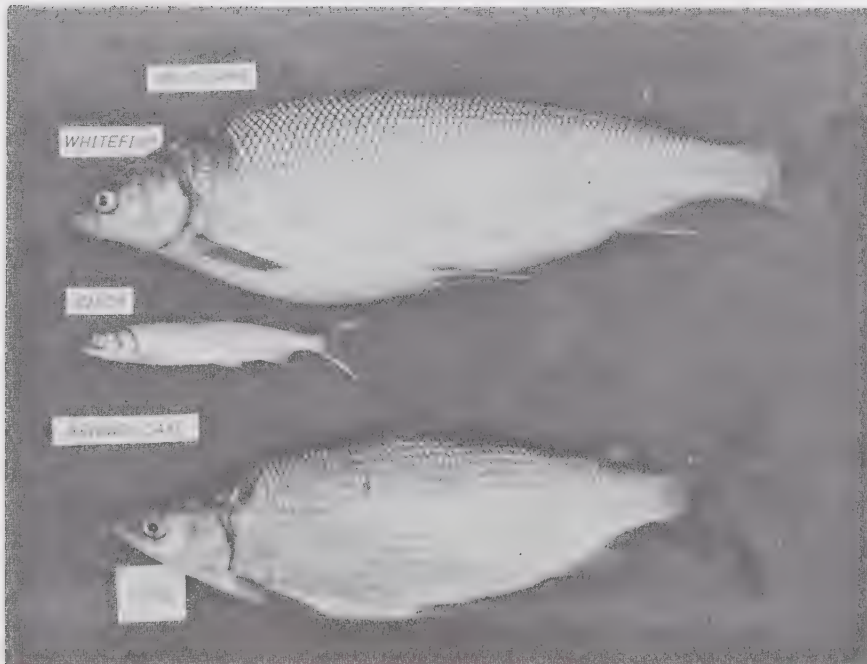
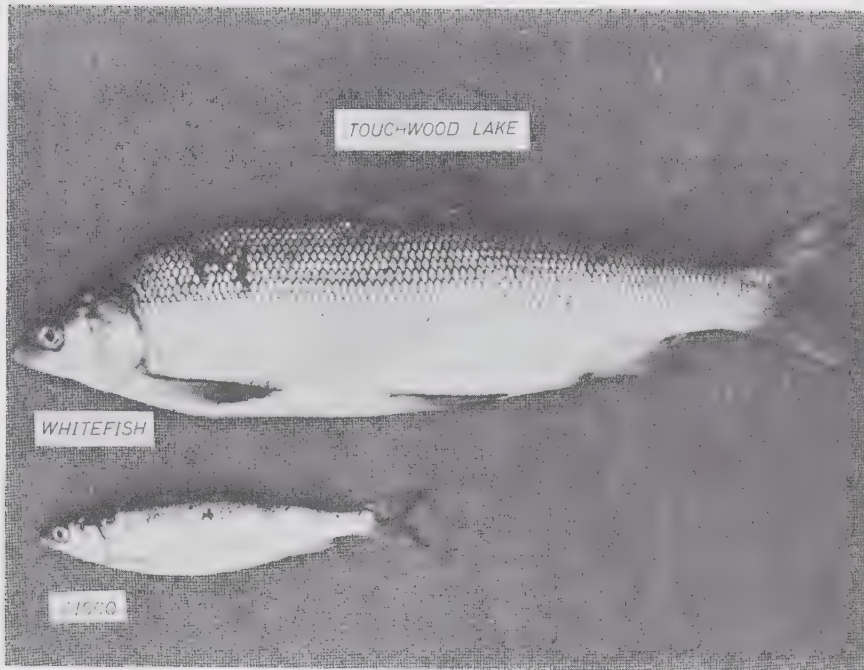
spawning acts of lake whitefish and cisco virtually no information was obtained in this study as to whether this is so in these species.

In the Utikuma River where spawning acts were observed, the species could not be distinguished in the dim light under which the observations were carried out. Attaching different colored plastic markers to the two species was attempted but fish handled in this way were not seen again on the only spawning area which was favorable for carrying out visual observations.

Nelson (1968) comments on the matter of size differences affecting mate selection, and on Hanson's reference to the fact that *Oncorhynchus nerka* tend to select mates of about their own size. This may be an important factor in sympatric populations of *C. clupeaformis* and *C. artedii* where one of the species is dwarfed. In Touchwood Lake and Cold Lake as previously noted, and as shown in Figure 55 and 56, the cisco adults are very small in relation to adult lake whitefish. No evidence of hybridization was obtained in these lakes. In Utikuma, Nipisi, North Buck and Unnamed Lakes, and to a lesser extent in Wolf Lake (Tables 4 - 6), the mature ciscoes approach adult whitefish in size and hybridization has been shown to take place.

FIGURE 55. Adult lake whitefish (S.L. 380 mm.) and adult cisco (S. L. 182 mm.) from Touchwood Lake.

FIGURE 56. Adult lake whitefish (S.L. 391 mm.) and adult cisco (S. L. 175 mm.) from Cold Lake. (Adult cisco from Kehiwin Lake for comparison.



Considering the nature of the spawning act itself as described by Fabricius and Lindroth (1954) in *C. lavaretus* and which is almost identical to that observed in this study, it is difficult to visualize how adult ciscoes of 175 to 210 mm. in length and of very slight body proportions could successfully engage in the act with adult lake whitefish of 375 mm. or more in length, and of much heavier body proportion. However, while size may be significant in maintaining reproductive isolation where one of two sympatric species is dwarfed, such an isolating mechanism does not have a genetic basis. It has been shown that dwarfing in whitefishes is due to environmental pressures (Svardson 1965).

A morphological characteristic related to spawning in whitefishes and one which may have a bearing on promoting conspecific matings is the difference in pearl tubercles in lake whitefish and ciscoes. Vladykov (1970) describes the type and location of pearl tubercles found on *C. alpeaformis* and on *C. artedii*. A large number of specimens captured during the spawning season in this study were examined for the presence of tubercles and findings were in general agreement with those of Vladykov. It was noted, however, that the tubercles of ciscoes, both male and female, were in nearly all cases scarcely visible except on close inspection and could scarcely be detected

by touch. On lake whitefish on the contrary, the tubercles were so prominent as to make the specimens very rough to the touch and in appearance. This applied to both males and females but more so to males. Mature hybrid males had well developed tubercles but not to the extent found on lake whitefish males while hybrid females resembled ciscoes in tubercle development. Fabricius and Lindroth (1954) suggest a functional role for tubercles in *C. lavaretus*, that of helping the pair remain in contact with each other during the spawning act. They speculate further that tubercles could serve as visual signals for spawning fish. Both of these suggestions seem logical and if tubercles do indeed serve such functions the marked differences in tubercle development in lake whitefish and ciscoes could quite readily be a factor in encouraging conspecific mating.

D. Hybrid Embryo Mortality

The mortality during the incubation period can be considered from time of fertilization up to a period of 80 days. Beyond that the results must be viewed with reservation because of the heavy mortality experienced during the time that the eggs were transferred from trays to jars. It is not known whether all lots were equally affected by the conditions imposed on them in

the jars and it is not known how much of the mortality which occurred subsequent to the eggs being returned to tray incubators, was due to the severe conditions associated with several days of jar culture.

During the 80 day period of incubation there was a wide difference in mortality between lots of the same cross. In a number of cases this difference exceeded the difference observed between lots of different crosses. There are a number of reasons why this might be so, i.e. difference in viability of eggs or sperm from different parents, difference in air temperature conditions during fertilizations (a temperature drop from 32° F to 10° F was experienced during collection of spawn at Utikuma Lake), difference in transportation time of some lots of eggs from fertilization site to the laboratory, (some lots were transferred within 24 hours while others did not reach the laboratory until 36 hours had elapsed.)

In calculating the percentage mortality during the aforementioned 80 day period, only total mortality of lots of the same cross was considered. These data are presented in Table 7.

It is difficult to interpret the data provided in Table 7. The two lowest mortalities experienced were in the lake whitefish female X cisco male cross from Touchwood Lake.

TABLE 7. Percentage mortality in artificial breeding experiments involving lake whitefish (W), cisco (C) and hybrids (H), during an 80 day period of incubation.

ORIGIN OF PARENTS	TYPE OF CROSS ₁					
	WXW	CXC	WXC	CXW	HXW	HXC
Touchwood L.	-	-	-	6.7	-	-
Utikuma L.	7.9	11.7	29.1	15.4	3.2	16.9

1 Male parent designated first.

Whether the highest mortality figure recorded in the lake whitefish male X cisco female cross is due to the smaller egg size of cisco female or some other factors, cannot be determined without repeating the experiments under more rigidly controlled conditions.

The single heterospecific cross using Touchwood Lake parents was made primarily to determine whether the apparent absence of hybrids in this lake is due to incompatibility of the eggs and sperm in the parent species. The high percentage of fertilized and developing eggs coupled with the low percentage of mortality during the 80 day period following fertilization indicate that incompatibility of cisco sperm, and whitefish eggs is not a factor in preventing hybridization. The reciprocal cross was attempted but not included in the data because cisco females were not ripe when the artificial spawning operations were carried out. However, a few eggs were obtained from one female by exerting heavy pressure on her body and these were fertilized with lake whitefish sperm. Several of these eggs developed and hatched which indicates that even when using a female fish that was not ready to spawn, crossing is possible and there is compatibility between cisco eggs and whitefish sperm as well.

The number of fry successfully hatched from each cross is presented in Table 8.

TABLE 8. Numbers of fry hatched in artificial breeding experiments involving lake whitefish (W), cisco (C) and hybrids (H). Percentage hatched in parentheses.

ORIGIN OF PARENTS	TYPE OF CROSS ₁				
	WXW	CXC	CXW	WXC	HXW HXC
Touchwood L.	-	-	3229 (41.2)	-	-
Utikuma L.	2991 (50.8)	4612 (29.2)	1677 (28.5)	4131 (25.5)	1952 (49.8) 4114 (39.0)

1 Male parent designated first.

As previously indicated, comparison of percentages of fry hatched between the various crosses is probably not valid. However, the data indicate that even with the severe abnormal mortality of eggs in the jars, hatching success ranged between 25.5 per cent and 50.8 per cent. The potential, therefore, exists in nature for heterospecific crosses, and backcrosses between some male hybrids and parental females of both species. The fact that progeny of all crosses were successfully reared in outdoor ponds further indicates that the expectancy of survival beyond the fry stage is good.

In the 1969-70 artificial breeding trials no wild hybrid females were obtained to determine the viability of their eggs. However, in the 1970-71 and 1971-72 spawning seasons several ripe hybrid females were obtained and their eggs were fertilized with both *C. clupearformis* and *C. artedii* sperm. Additionally in 1971-72, two ripe male hybrids were obtained and hybrid female eggs were fertilized with hybrid male sperm. In the 1970-71 trials, the two lots of female hybrid eggs (one fertilized with *C. clupearformis* sperm, the other with *C. artedii* sperm) all died within 21 days after attempted fertilization.

The results of the 1971-72 trials are shown in Table 9.

TABLE 9. Record of egg mortality during incubation, and hatching success of hybrid (H) X hybrid cross and hybrid females backcrossed to *C. clupearformis* (W) and *C. arctedii* (C) males.

PARENTS ₁	NO. OF EGGS IN SAMPLE	PER CENT MORTALITY	PER CENT REACHING EYED STAGE	PER CENT HATCHED
WXW	863	9.0	93.50	91.0
CXC	1939	7.50	95.0	92.50
CXH	1561	100.0	0.0	0.0
CXH	1834	100	0.0	0.0
WXH	1961	100.0	0.15	0.0
WXH	1610	99.94	0.06	0.06
HXH	1864	99.95	0.21	0.05
HXH	1549	100	0.0	0.0
HXH	1565	100	0.0	0.0

1 Male parent designated first.

It is evident that the viability of female hybrid eggs is extremely low. Only 8 of 11,944 of these eggs reached the eyed stage and only two individuals hatched. The *C. clupeaformis* and *C. artedii* controls, on the other hand, had a hatching success rate of over 90 per cent. During the trials, it was noted that by the 9th day after incubation began, the majority of eggs of hybrid female origin, regardless of the type of male parent used in the cross, had become whitish and opaque in appearance while the controls had the color and appearance of normally developing eggs. Periodic examination of eggs of the various crosses under a binocular microscope revealed no development in these eggs of hybrids which had become cloudy in appearance, while development progressed favorably in the controls.

The two individuals that hatched from hybrid eggs died while attempts were being made to rear them. One died on the 28th day and the other on the 65th day after hatching. The cause of mortality of these fry is not known. They had been feeding in what appeared to be normal fashion compared to the controls.

E. Hybrid Sterility

In examining the gonads of wild adult hybrids, it was noted that a number of these fish showed no gonad development. Invariably such specimens had large amounts of fat in the body cavity. The sex of these animals could not be determined, as what appeared to be gonad tissue was nothing more than a thin elongate tube. In the hybrids which showed considerable signs of maturing, abnormality was evident in both the males and to a lesser extent in the females. In males particularly, it was not unusual to find only one testis or only part of one testis showing development. A record of gonad development in the wild hybrids from the lakes under study is presented in Table 10.

The pattern of gonad development in hybrids is somewhat erratic. The percentage of these fish which showed no development (sex could not be determined) varied from 25 per cent in Wolf Lake to almost 58 per cent in Nipisi Lake. A high percentage of male fish which do mature, show abnormal gonad development and this is also true for females in Utikuma and Nipisi Lakes. However, in North Buck and Wolf Lakes all females which matured, appeared to have normal gonad development. No mature *C. clupeaformis* or *C. artedii* males or females examined in this study showed lack of, or abnormal gonad development.

TABLE 10. Percentage of wild adult hybrids having no gonad development and percentage of mature hybrids of both sexes showing abnormal gonad development.

LAKE OF ORIGIN	NUMBER OF SPECIMENS	PER CENT NO DEVEL.	PER CENT MATURE ♂ ABNORMAL	PER CENT ♀ MATURE + ABNORMAL
Nipisi	19	57.9	66.7	60
North Buck	35	34.3	42.9	0
Ut ikuma	42	33.3	54.6	35.3
Wolf	20	25.0	69.2	0

DISCUSSION

A. Observed and Probable Extent of Hybridization

Hybridization between *C. clupeiiformis* and *C. artedii* was found in five lakes in the Mackenzie and Hudson Bay drainage basins. While these lakes represent some variety in lacustrine habitats, they are also similar in that they have relatively shallow basins, are generally eutrophic in nature and are essentially isothermal during the open water season. The east arm of Wolf Lake is an exception, being comparatively deep and thermally stratified during the summer.

During the course of this study, the opportunity to examine whitefish intermediate between *C. clupeiiformis* and *C. artedii* from a number of other lakes within the area of sympatry, together with information obtained from fishermen, suggests the presence of hybrids in at least four other widely separated lakes in the same drainage systems. Although this evidence along with the previously cited reports of the occurrence of hybrids in the Great Lakes, northwestern Ontario, Manitoba and Saskatchewan (R.P. Johnson pers. comm.), indicates that hybridization is widespread throughout the zone of sympatry, this work reveals that the incidence in any one environment relative to the parent species, is low. In Alberta lakes where adults of both parental species are similar in size, the chances of hybrids occurring seem quite likely.

Some specimens are difficult to classify. Morphometrically these individuals are found between hybrids and ciscoes. Such specimens are rare but at least some of them are believed to represent backcrosses between hybrid males and cisco females. If backcrossing were common, more doubtful individuals should have been present in the samples.

Even though hybridization is not now believed to be a rare occurrence in Alberta, this does not mean that *C. clupeaformis* and *C. artedii* are not full species. The parent species have remained distinct and species integrity is being maintained. The status of these two whitefishes as separate species has not been questioned, but on the matter of whether they represent separate genera, there has been some disagreement. Behnke (1972) supports the current taxonomic position of one genus for lake whitefish and ciscoes, but favors differentiation at the subgeneric level, i.e. subgenus *Coregonus* for whitefish and subgenus *Leucichthys* for ciscoes. His reasons for doing so in part, are "the frequency of natural hybrids between ciscoes and whitefish and the high fertility of the hybrids". As noted above, experimental evidence obtained in the present study is not in agreement with the high fertility of the hybrids concept, at least as far as *C. clupeaformis* x *C. artedii* hybrids are concerned. However, since there is at least partial fertility in male hybrids and backcrosses are possible, the present work does not present enough new evidence to argue that

these species should be placed in separate genera.

B. Causes of Hybridization

The eutrophic nature of the lakes in which hybrids were found and which is referred to above, may have implications in causing hybridization. These environments tend to produce a larger cisco either because of increased productivity of eutrophic lakes generally or, possibly, for other reasons not well understood at this point. It has been shown that it is only when the adult ciscoes are approaching lake whitefish in size that hybrids are produced.

Disproportionate numbers of the parent species has been cited by Hubbs (1955), and Hubbs and Laritz (1961) as a factor leading to hybridization. The reason that this situation is conducive to hybridization is that individuals of the scarce species are unable to find a conspecific mate and are, therefore, more apt to mate with an individual of a related species. In Unnamed Lake, Nipisi Lake and Wolf Lake, hybrids made up an estimated 0.7, 2.3 and 3.1 per cent of the coregonine population respectively. Numbers of lake whitefish are relatively scarce in relation to ciscoes in all three lakes yet the incidence of hybrids is low. In Utikuma Lake on the other hand the ratio of lake whitefish to ciscoes is much more evenly balanced and the incidence of hybrids (6 per cent) is the highest found in the study. (North

Buck Lake was not included in these considerations because of limited data obtained from it.) Disproportionate numbers of parent species does not seem to be the main cause of hybridization in this investigation.

Disturbances in the environment such as construction of dams, fluctuation in water levels, drainage diversions, etc. have been identified in other studies as factors inducing hybridization (Hubbs, 1955). No significant physical disturbances of the lakes or their drainage systems have occurred either in those in which hybrids were found or in those in which hybrids were not recorded. Commercial fishing may be considered to be a disturbance of the normal biological relationships in the environment and could be a factor in causing hybridization, although no reference to this was found in the literature. Fishing is carried on in those lakes which lack hybrids as well as in the lakes in which hybrids occur. Furthermore, a single hybrid specimen was obtained in a relatively small sample of coregonines from Unnamed Lake where no commercial fishing has ever been undertaken. Man-made changes in the environment cannot be considered to have played a part in this hybridization process.

The introduction of one or both parental species into a new environment may be another cause of hybridization (Hubbs and Hubbs, 1947). This is not applicable to the lake whitefish and cisco populations in this work.

Nelson (1968) considered whether restriction in the size of the spawning area might force species to mate within close proximity to each other. The spawning areas used by lake whitefish and ciscoes were usually extensive in area and in all lakes investigated, more than one area was used. There was one exception to this: the spawning area in the Utikuma River just downstream from the highway bridge where on occasions more than one hundred ripe lake whitefish and cisco could be taken in a single seine haul from an area of sand and gravel in the river bed, no larger than 150 square yards in extent. Crowding of spawners on small areas such as this could quite conceivably lead to accidental crossfertilization (Hubbs, 1955). It should be pointed out that there are other extensive spawning grounds in Utikuma Lake which are also utilized by both species but where such congestion of spawners probably does not take place.

The main causes of hybridization appear to be incomplete isolating mechanisms between the two species. As previously indicated, both temporal and habitat isolation are virtually non-operative in the lakes where hybrids occur. This leaves ethological isolation as probably the most important mechanism involved in preventing hybridization in some cases and in reducing the amount of hybridization in others. Mayr (1963) considers ethological barriers to be important in most

species. No experimental evidence to support the importance of ethological isolation was obtained, but the absence of hybrids where a great discrepancy in the size of adults in the two species exists would strongly suggest a behavioral barrier during spawning. The differences in the development of nuptial tubercles in the two species has been mentioned as a possible basis for species recognition and, hence, conspecific mate selection.

With regard to postmating isolating mechanisms, there is no evidence in these data that embryo mortality in hybrids is any greater than that in homospecific crosses. Garside and Christie (1962) whose experiments were not subjected to an abnormal mortality during incubation, also report that hybrid embryos of *C. clupearformis* X *C. artedii* and the reciprocal cross had survival rates as high as that of homospecific crosses. Survival to hatching of hybrids from Touchwood Lake (dwarf-type cisco male X normal lake whitefish female), was also high, hence, it can probably be concluded that the results of making interspecific crosses with allopatric parents would have been as high as those involving parents from sympatric situations.

Hybrid sterility, and partial sterility due to abnormal gonad development, has been shown to be an effective although not complete block to backcrossing. The fact that some male hybrids are capable of fertilizing eggs of either parent, allows for the

production of backcrosses, but since hybrids form a relatively small percentage of the coregonine population, the chances of male hybrid matings with either female parent would be low in comparison to the chances for conspecific mating.

C. Consequences of Hybridization

Swamping or introgression of the parental species has not occurred in any of the situations investigated. The parent species in the five lakes appear to have remained as distinct as those where no hybridization has taken place and as distinct as those from allopatric populations. Intermediate forms which probably are present intermittently throughout the zone of sympatry of *C. clupeaformis* and *C. artedii*, are probably mostly F₁ individuals, and are likely to be found in lakes where adults of the parent species are more or less of comparable size. Since it cannot be demonstrated that hybridization has been induced through man's interference, it is likely that it has been occurring in areas where the two species became sympatric after the last glaciation.

For swamping to occur, the hybrids must be at a selective advantage. This can scarcely be said to be the case since female sterility and lack of gonad development must seriously impair the possibility of gene flow. As previously mentioned, there is an opportunity for gene flow through F₁ males mating with females of the parent species. Evidence produced

here and also put forward by Svardson (1965) shows that the F_2 's have greater variability than the F_1 's and the parent species, hence, it is likely that many of these individuals would be poorly adapted and their survival would be impaired in the natural environment. If this is, in fact, the case, it would further contribute to the blockage of gene flow. It is not known whether backcrosses (F_2 's) are fertile or whether gonad development in this generation is interfered with due to their unbalanced gene complexes. It can only be said that very few individuals are likely to be present in a population and any abnormality that may occur would further reduce their opportunity to contribute to gene flow. If the doubtful individuals found in this study are backcrosses, there must be selection against them contributing further to gene exchange since swamping would have had time to take place since the species came into sympatry.

The fact that hybrid fertility is quite reduced as compared with that claimed by European workers working with other coregonine species, suggests that *C. clupeaformis* and *C. artedii* have diverged to a greater extent prior to coming into contact, and that speciation is more complete than in some European cases which have been reported.

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